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A Description and Analysis of Behavior Patterns Among Uinta Ground Squirrels

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A DESCRIPTION AND ANALYSIS OF BEHAVIOR PATTERNS AMONG UINTA GROUND SQUIRRELS

by

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of

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Approved:

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Thomas E. Morse

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ABSTRACT

A Description and Analysis of Behavior
Patterns Among Uinta Ground Squirrels

by

Thomas E. Morse, Doctor of Philosophy

Utah State University, 1978

Major Professor: Dr. David F. Balph
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This research describes and analyzes the behavior of free-living Uinta ground squirrels (Spermophilus armatus) temporally, spatially and with reference to differences in sex, age, population density and habitat. In addition, the relationships between local meteorological parameters and time spent above ground are described and analyzed.

The frequency of eight behaviors, feeding, moving, encounters, upright, motionless, grooming, nest gathering and calling, among ground squirrels was found to be labile, varying in frequency with time of day, period of the season, sex, age, population density and habitat, and varying in spatial distribution within the home range.

The dominant behavior, feeding, was most frequent during the first and last two hours of the day and tended to occur within the home range core during these hours. During the midday periods home range use became more general and the frequency of the other behaviors increased as feeding frequency decreased.

During periods of sexual activity (the beginning and end of the homeothermic season), male ground squirrels displayed high frequencies

of encounters, moving and calling behaviors. During the midperiod of the season males increased the frequencies of feeding, grooming and nest gathering. The lactation period was the period in which most behaviors peaked in frequency among females. The frequencies of moving, upright, nest gathering and calling all had seasonal peaks during lactation. Between sexes, males tended to exhibit higher frequencies of behaviors that contributed to social interaction than did females, and females tended to exhibit higher frequencies of behaviors that contributed to self-maintenance and productivity than did males. Few consistent differences in frequency of behavior were observed between age groups of the same sex.

Home range size varied seasonally and with sex of the squirrel. Home ranges of males were large during periods of sexual activity and small during the postbreeding period. Home ranges of females tended to increase in size as the season progressed. Among all squirrels, moving tended to be peripherally distributed within the home range. Because of the large amount of individual variation in the spatial distribution of specific behaviors within the home ranges of groups of like squirrels it was concluded the distribution of behavior within the home range of an individual was likely to be a result of the unique distributions of physical and social characteristics of its home range.

Frequency of behavior and spatial distribution of behaviors within the home range were also related to population density among ground squirrels. During years of high population density females exhibited higher frequencies of behaviors that could be related to

aggression than they did during years of low population density. These differences in behavior frequency among females are consistent with the greater intolerance of conspecifics by females than by males, hence their greater sensitivity to high population numbers. Among all squirrels the distribution of specific behaviors tended to become less proportional to the distribution of home range use as effective density about the home range increased.

Distribution of behavior within the home range and distribution of use within the home range were correlated with the spatial distribution of encounters initiated by neighbors upon a home range resident and the distribution of encounter losses within its home range. Maintenance of a given home range appears to be related to the frequency of encounters won within the core area.

Time spent above ground by squirrels was correlated with the seasonal variation in ambient temperature and heat exchange between the individual and its environment. During the first 40 days of the 1970 season activity tended to increase as ambient temperature or heat gain increased. Thereafter activity was negatively correlated with ambient temperature and rate of heat gain. The principal mode of thermoregulation appeared to be behavioral, i.e., avoiding heat and water stress by use of alternative microhabitats, principally the burrow, as sinks for the dissipation of heat. It is believed that the seasonal variation meteorological factors with the attendant changes in quantity and quality of foods to be the prime factors influencing the length of the homeothermic season.

The strategies squirrels use to increase individual fitness and the implications of this research with regard to estimating population density, predicting effects of habitat manipulation and management of squirrels at rehabilitation sites are discussed.

(213 pages)

INTRODUCTION

The manner in which animals apportion their behavior in time and space is of interest to biologists. This is because animal behavior often appears in temporal and spatial patterns, which in turn may be related to social, physiological and environmental circumstances of the animal (Craig 1918, Brown and Orians 1970, Enright 1970, Marler and Hamilton 1966). With a description of these relationships, better inferences may be made about factors that influence distribution and abundance of a species. For example, the functional relationships between behavior and some environmental parameters may be determined (Post 1974), the functional use of space by a species may be determined (Brown 1975), or the intrinsic tie between the animal and the meteorological characteristics of its environment may be better understood (Moen 1973, Morhardt and Gates 1974).

In addition to being of interest to biologists, time and behavioral-use-of-space studies are also of value to wildlife managers. This is because the ability to census, predict impact responses, or to restore a population to its former distribution and abundance is based upon knowing an animal's responses to a variety of biotic and abiotic factors. The study of time budgets of sex and age groups helps to determine those critical periods of a species' life cycle most susceptible to manipulation and those sex and age groups that would be most affected by population manipulation or habitat modification. Time budgets, when expressed as a correlation between time spent in an area and the thermal characteristics of that

area, assists the manager in determining habitats whose thermal characteristics are within the species' thermoregulatory capacities. Spatial analysis of behavior assists the manager in determining those factors which influence dispersion of sex and age groups within an area, dispersal of animals from an area, and the manner in which animals use space.

Despite the utility of studies of time-budgets and behavioral-use-of-space, these areas of research tend to be restricted to large mammals, birds and lizards. Few descriptions of this type have been made of small mammals in the wild because of the difficulties encountered in observing the animals or estimating their metabolic rates. This study attempted to add to our knowledge in these areas using the Uinta ground squirrel (Spermophilus armatus).

Uinta ground squirrels are well suited for research on time-energy budgets and behavioral use of space. They are diurnal, easily trapped, have small home ranges and acclimate well to observation. Their small size suggests that they should be particularly sensitive to thermal stress. Spermophilus spp. are widespread in North America and should share many of the physiological and social attributes of the Uinta ground squirrel. Thus, the information gained from this study may have broad applicability. In addition, the montane habitats occupied by the Uinta ground squirrel in Utah, Idaho, Montana and Wyoming are being developed at an increasing rate, so that research on this species should be of particular value to resource managers attempting to assess the impact of various man-related activities upon the environment.

Specific objectives of this research were:

1. To describe and compare diurnal and seasonal behavior of ground squirrels with reference to differences in age, sex, population density and habitat.

2. To describe the diurnal and seasonal variation in meteorological parameters of the study site and determine the relationships between these factors and the time spent above ground by male and female ground squirrels.

3. To describe and compare the manner in which ground squirrels use space within their home ranges with reference to differences in age, sex, effective density and habitat.

GENERAL PROCEDURES

This research was part of a broader seven-year investigation into the behavior and ecology of a population of free-living ground squirrels. The principal objective of the parent investigation was to define the role of behavior as a mechanism of population regulation. Two situations were studied. A naturally occurring population of 23-28 yearlings and adults per hectare was studied during 1964-1967 (high density) and a manipulated population of 11-14 yearlings and adults per hectare was studied during 1968-1970 (low density). The data used in this research were collected on yearling and adult ground squirrels during the spring and summer of 1965, 1966, 1969 and 1970.

The study site was located on 8.9 ha of land surrounding the Utah State University Forestry Field Station 32 km northeast of Logan, Utah, at an elevation of 1,921 m. In the center of the study area were 1.1 ha of lawn and roadways surrounding the building of the station. The remaining area was vegetated by discontinuous patches of field, brush and forest (Balph and Stokes 1963, Walker 1968).

Each year an attempt was made to capture and mark all squirrels every ten days. In addition to a permanent toe clip, each captured animal was marked with black Nyanzol dye to facilitate field identification. The time, location, identity, age, sex, body weight, and overt reproductive status were recorded each time an animal was captured. Location was determined from a 12.19 m grid system established on the area.

Six areas were selected and used as sample areas for data collection. At each sampling area a tower four meters high was erected. The above-ground activities of squirrels were recorded from these towers. Standard daylight military time was used as the base for recording daily activity. Seasonal time was recorded in days since the emergence (D.S.E.) from hibernation of the first squirrel.

Time budgets of ground squirrels were defined at two levels. These were the proportion of time spent in each of the eight behaviors studied and the time spent above ground without reference to specific behaviors.

Activity of squirrels was sampled throughout the period of diurnal activity following their emergence from hibernation. At each sampling area one complete diurnal period of activities was recorded each 10-day interval. Behaviors were recorded sequentially on three data forms: scans, encounters and sightings. Each sequence required 10 to 15 minutes to complete.

The information recorded during a scan was the location, identity, sex, age, and behavior of squirrels within a control grid assigned to each of six towers. Upon completion of the scan, all encounters occurring within the grid assigned to the tower during five minutes were recorded. The recorded information for each encounter was the location, identity of the initiating squirrel, outcome of encounter, occurrence of contact in aggression, occurrence of chase in aggression, distance between individuals at the time of initiation, and the identity of the other encounter participant.

Immediately following the encounter sampling, sightings of the location, identity, sex, age and behavior of every animal visible from the tower were recorded. When sightings were completed, a new sequence was begun. Time of day and D.S.E. were recorded for each data entry. The behaviors recorded were feeding, moving (running), encounters, upright, motionless, grooming, nest gathering and calling. These behaviors are described by Balph and Stokes (1963).

The above-ground season of each sex was divided into three periods: the gestation, lactation and postweaning periods for females and the breeding, postbreeding and fall periods for males. The gestation and lactation periods were determined from weight data and nipple condition of each female. The postweaning period was defined by the interval between nipple regression and entrance of the female into aestivation-hibernation. The breeding period of each male was defined as that interval between spring emergence and gonadal regression. The postbreeding period was defined as that interval between spring gonadal regression and late summer gonadal recrudescence. The fall period was defined as the interval between late summer gonadal recrudescence and entrance into aestivation-hibernation.

RESULTS AND DISCUSSION

Annual Cycle

Emergence from hibernation by the first ground squirrel at the Utah State University Forestry Field Station occurred between March 28 and April 16 during the years 1965 through 1970. With the exception of 1965, a late year, squirrels emerged in sequence of adult males, adult females, yearling females and yearling males (Slade and Balph 1974). Females were bred within a few days after emergence and gave birth approximately 26 days later. Juveniles emerged from their burrows about 24 days after birth and were independent of the natal burrows about 15 days later. Adult ground squirrels began entering hibernation in July and all squirrels had disappeared by early September. The annual cycle of individual Uinta ground squirrels is composed of two seasons. A homeothermic season of approximately 3.5 months followed by an endothermic season of approximately 8.5 months.

Time Budgets

Introduction

Despite the extensive volume of literature available on small mammals, there is a general lack of comprehensive descriptions of how individuals in a wild population appropriate their time (Hinde 1970, Gessaman 1973, King 1974). This portion of the research was an attempt to add to our knowledge of the time budgets of small

mammals through studies of the Uinta ground squirrel. The objectives of this research were (1) to describe the variation in time spent in specific behaviors by ground squirrels between periods of the homeothermic season and between periods of the day, then (2) to determine if differences existed in the time spent in specific behaviors between males and females, adults and yearlings, years of differing population density, and habitat types.

Relative amount of time spent in specific behaviors

The relative amount of time spent by ground squirrels in the eight behaviors during the years 1965, 1966, 1969 and 1970 was determined (Table 1). The most common behavior of ground squirrels during these four years was feeding (53 percent of 54,597 observations). The second, third, and fourth most commonly exhibited behaviors were moving (19 percent), motionless (10 percent), and upright (9 percent). The remaining behaviors, encounters, grooming, nest gathering, and calling, were all exhibited at relatively low frequencies (each behavior was observed less than 4 percent of the time).

Relative time budgets have little utility other than to give one a basic idea of how the species apportions its time in the various behaviors studied. Therefore, in the remaining portions of time budget analysis I will examine in sequence the possible relationships between the time spent in the eight behaviors by ground squirrels and 1) reproductive period of the homeothermic season, 2) time of day, 3) sex, 4) age, 5) population density, and 6) habitat.

Table 1. Relative amount of time spent in eight behaviors by Uinta ground squirrels during the years 1965, 1966, 1969 and 1970.

	Behavior								
	Feeding	Moving	Encounters	Upright	Motionless	Grooming	Nest Gathering	Calling	Total
Frequency	28,876	10,173	1,121	5,055	5,503	1,778	1,145	646	54,597
Percentage	52.9	18.6	2.1	9.3	10.1	3.3	2.6	1.2	100.1

Comparisons of time budgets among ground squirrels

Data used for time budget analysis were the scans and sightings made during 1965, 1966, 1969 and 1970. Observations were grouped on the basis of sex and age of the squirrel, the 10-day interval it emerged from hibernation and the year of observation. These data were further segregated on the basis of reproductive period of the season. Comparisons were then made of the relative frequencies in which the eight behaviors were displayed within a group of squirrels during different time periods or between different squirrels during similar time periods.

I used the independence chi-square contingency analysis to test for significant differences in relative frequency of these comparisons. This type of analysis was used because the data were nonparametric and the analysis is appropriate for assessing proportional differences. The total chi-square value with appropriate degrees of freedom was used to determine if there were significant differences in relative frequencies of the eight behaviors in a comparison. Secondly, the contribution to chi-square associated with each column of the contingency table was used to identify those specific behaviors whose relative frequencies were significantly different.

The next step in analysis of time budgets was to determine if there were consistent patterns in the proportion of time spent by squirrels in specific behaviors between comparison sets. A comparison set is defined here as the relative frequencies in which the eight behaviors were displayed within a group of squirrels during a day or for the three seasonal periods or between different classes of

squirrels during similar time periods, i.e., a data set for a contingency table. For example, if the feeding frequency of adult males in 1966 increased significantly each period of the season it would be of interest to know if feeding frequency increased each period of the season among all groups of males during all years.

To facilitate the determination of consistent patterns of frequency of specific behaviors among comparison sets, I adopted an ordinal scale by which the differences in frequency of specific behaviors in any comparison set could be objectively represented and compared directly to frequency differences of the same behavior in all other comparison sets. This was done by assigning each cell value in the contingency tables (comparison sets) a symbol to represent the deviation from the expected value. If the contribution to chi-square associated with that cell was larger than the product of the total number of degrees of freedom of the contingency table divided by the number of cells in the contingency table times 3.84 (the critical chi-square value at an alpha level of .10 with 1 degree of freedom), then the cell was assigned a plus or a minus sign depending on whether or not the observed cell frequency was larger or smaller than the expected cell frequency; otherwise no symbol was given. Thus patterns of the proportion of time spent in specific behaviors were represented by sequences of symbols. For example, if the frequency of feeding during the breeding, postbreeding and fall periods of a season by a group of squirrels increased significantly each period, the symbol sequence would be a minus, followed by no symbol, followed by a plus. If there were no

differences in feeding frequency by a group of squirrels during the season, the symbol sequence would be the absence of any symbols.

Consistent patterns of the proportion of time spent in specific behaviors were determined by the number of times a symbol sequence of a general pattern occurred among comparison sets. A general pattern of frequency incorporates those symbol sequences that could be interpreted as having the same general trend. For example, a general increase in feeding frequency by a group of squirrels during three different periods of the season could be represented by the symbol sequences - o +, o o +, - - +, o + + or - + +. No attempt was made to apply a statistical test to determine the most consistent pattern of frequency of specific behaviors among comparison sets, since the frequency in which a given symbol sequence occurs is markedly influenced by the alpha level chosen as significant in the contingency table.

Once the chi-square analysis was completed and the symbols assigned to each cell, the frequencies of specific behaviors were converted to percentage values. These percentage values are used to display the frequency data of comparison sets.

The results of time budget analysis are reported in a two-step sequence. First, the number of comparison sets those relative frequencies of the eight behaviors were significantly different between categories of a comparison are reported. The total chi-square value of the contingency table was used to determine if there were significant differences in the eight behaviors of a comparison set. Secondly, the consistent patterns of the proportion of time spent in

specific behaviors by squirrels within all the comparison sets are enumerated.

Seasonal organization of behavior among males. Within 17 groups of males whose behaviors were compared between periods of the season, 16 groups apportioned their time spent in all eight behaviors differently each period of the season ($P<.10$) (Table 2). Thus, it appears likely that the behavior of male ground squirrels is temporally organized with regard to periods of the homeothermic season.

When enumerating consistent patterns of frequencies of specific behaviors during the three seasonal periods, I enumerated only five general patterns of frequency. These five general patterns of frequency of specific behaviors were 1) no differences in frequency between periods of the year, 2) a general decrease in frequency as the season progressed, 3) a general increase in frequency as the season progressed, 4) a peak in frequency during the midperiod of the season, and 5) a frequency low during the midperiod of the season.

Seasonal patterns of frequency of specific behaviors among the 17 groups of males were variable (Table 2).

The most consistent seasonal pattern of frequency of feeding, motionless and upright behaviors among the 17 groups of males was no difference in frequency between periods of the season. Nine of 17 groups of males showed this pattern of feeding, 10 groups showed this pattern of motionless behavior, and 11 groups showed this pattern of upright behavior. Those groups having significant

Table 2. Comparisons of the relative frequency of eight behaviors within groups of male Uinta ground squirrels during the breeding, postbreeding and fall periods of the 1965, 1966, 1969 and 1970 seasons. Behavior frequencies displayed as percentage.

			Behavior								
Year	Group	Period	Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1965	Ad. 0-9	Breed.	41.4-	37.4+	3.5	4.9	6.8	1.0-	0.3-	4.7+	1093
		Post.	58.0+	17.2-	1.7	7.1+	6.6	3.6+	5.1+	0.7-	758
		Fall	54.2	30.1	3.2	1.1-	9.5	2.0	0.0-	0.0-	349
											2200
		Chi-sq.	27.2	62.9	5.1	16.9	3.1	14.3	63.5	38.8	231.8***
	Ylg. 0-9	Breed.	39.4	35.9+	6.5+	5.3	7.1	2.4	1.8-	1.8	170
		Post.	49.6	16.8-	2.5	4.1	11.7	4.8	9.2+	1.3	393
		Fall	47.4	30.4+	0.0-	0.7	14.1	2.2	4.4	0.7	135
											698
		Chi-sq.	2.7	20.7	11.1	4.5	3.7	3.0	11.1	0.6	57.4***
	Ylg. 10-19	Breed.	56.5	25.0	8.2+	2.2	2.6-	3.0	0.4-	2.2	232
		Post.	57.3	16.3-	2.2-	6.1	8.5	4.6	3.4+	1.4	410
		Fall	45.3	32.6+	1.1	4.2	15.8+	0.0	0.0	1.1	95
											737
		Chi-sq.	2.1	12.0	15.8	5.0	16.5	4.9	8.7	0.7	65.8***
	Ylg. 20-29	Breed.	46.4	20.8	7.2+	9.6+	8.0	4.0	1.6-	2.4	125
		Post.	48.8	16.3	2.6	2.9	12.8	4.9	10.5+	1.1	344
		Fall	49.3	26.1	0.0-	0.7-	16.4	2.2	4.5	0.7	134
											603
		Chi-sq.	0.1	5.0	11.6	15.0	3.7	1.7	11.8	1.5	50.3***
1966	Ad. 0-9	Breed.	40.0	33.3+	3.5	8.4	10.2	1.8-	0.2-	2.5+	1474
		Post.	44.5	23.8-	0.9-	6.8	10.7	5.4+	7.5+	0.4-	559
		Fall	36.8	29.2	4.7	1.9-	25.5+	1.9	0.0-	0.0	106
											2139
		Chi-sq.	2.6	12.1	11.0	6.2	20.7	18.7	105.3	12.3	188.8***
	Ad. 10-19	Breed.	33.0-	36.4+	3.7+	8.1	9.8	3.6	2.2	3.2+	786
		Post.	47.0+	20.0-	1.1-	9.0	14.7+	4.6	3.7+	0.2-	545
		Fall	47.8+	23.2	2.1	13.2	8.9	4.7	0.0-	0.0-	190
											1521
		Chi-sq.	19.1	32.4	8.6	4.2	7.9	1.1	7.9	20.6	101.8***
	Ylg. 10-19	Breed.	49.9	22.9	2.2	9.0	10.9	3.3	0.3	1.6	367
		Post.	46.1	23.3	2.9	6.7	13.9	4.8	1.9	0.3-	373
		Fall	31.8	31.8	4.5	4.5	18.2	0.0	0.0	9.0+	22
											762
		Chi-sq.	1.7	0.7	0.7	1.6	1.9	2.0	4.8	14.9	28.4*
	Ylg. 20-29	Breed.	53.4+	22.1-	3.0+	4.3-	12.3	2.6	0.4-	1.8+	494
		Post.	43.7	26.1	-.8-	9.4+	10.2-	5.7+	2.7+	1.4	662
		Fall	41.4-	30.1+	2.2	7.0	15.4+	2.5-	1.1	0.1-	718
											1874
		Chi-sq.	10.1	7.2	8.2	10.5	7.7	11.8	11.3	9.4	76.1***
	Ylg. 30-39	Breed.	43.6	31.5	1.7	3.7	12.7	4.0	1.0-	1.8	597
		Post.	37.5	26.7	1.5	6.4	14.9	5.5+	6.4+	1.1	469
		Fall	46.0	27.7	3.0	5.5	15.8	1.4-	0.3-	0.3	361
											1427
		Chi-sq.	3.9	2.4	2.9	4.1	1.7	9.2	39.4	4.7	68.4***

Table 2. Continued.

Year	Group	Period	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
1969	Ad. 0-9	Breed.	48.0	17.9	2.6	11.4	9.5	2.6	4.0	4.0	273
		Post.	44.8	19.0	1.0	17.1	5.7	4.8	6.6	1.0	105
		Fall	33.3	33.3	2.6	20.5	10.3	0.0	0.0	0.0	39
											417
		Chi-sq.	1.6	4.1	0.9	3.3	1.4	2.5	3.1	3.7	20.8
	Ylg. 10-19	Breed.	54.1	10.2	1.5	16.3	10.2+	5.6+	0.5-	1.5	196
		Post.	46.2-	15.2	0.7	26.6+	4.5-	1.3-	3.8+	1.8	448
		Fall	59.5+	14.8	1.1	14.0-	6.8	2.8	0.9-	0.0-	351
											995
		Chi-sq.	6.8	2.6	1.1	17.3	7.1	9.2	11.0	6.1	61.2***
	Ylg. 20-29	Breed.	48.7	18.7	4.2	11.3	11.9	2.4	0.6	2.4+	337
		Post.	49.0	19.5+	1.7	16.1	10.0	1.7	0.8	1.3	529
		Fall	62.5+	11.3-	3.6	11.3	9.5	0.9	0.2	0.7	443
											1309
		Chi-sq.	10.3	11.1	5.1	5.5	1.1	2.6	1.3	4.0	41.0***
	Ylg. 30-39	Breed.	41.8	19.4	4.1	17.3	12.2	1.0	0.0	4.1+	98
		Post.	41.7	32.8+	1.2-	12.6	6.9	1.6	2.0	1.2	247
		Fall	51.5	18.0-	7.0+	14.1	7.8	1.6	0.0	0.0	128
											473
		Chi-sq.	2.0	9.2	8.6	1.2	2.5	0.2	4.6	6.5	34.7***
1970	Ad. 0-9	Breed.	46.6	22.4	3.4+	10.5	14.3	1.1-	0.5	1.1	1144
		Post.	52.8+	18.5	0.9-	11.3	10.6-	3.5+	1.3+	1.2	1355
		Fall	45.3	22.4	2.5	10.1	16.4	2.5	0.0	0.7	585
											3084
		Chi-sq.	6.9	5.5	19.1	0.7	13.0	14.6	9.8	1.0	70.5***
	Ad. 10-19	Breed.	32.0-	15.5+	2.9	26.2+	11.7	1.9	1.0	8.7+	103
		Post.	58.5	7.5	0.0-	9.8	8.5	10.5+	2.4	2.7	294
		Fall	76.3+	5.0-	2.3	8.2-	5.9	1.8-	0.0	0.5-	219
											616
		Chi-sq.	23.0	9.9	7.5	21.0	2.9	19.3	5.6	16.5	105.8***
	Ylg. 0-9	Breed.	53.2	20.2	4.4+	6.9	10.1	0.4-	1.2	3.6+	248
		Post.	55.0	17.2-	0.7-	11.0	7.3	6.3+	1.8	0.6	615
		Fall	47.6	28.0+	2.4	7.5	10.7	2.2-	1.2	0.4-	496
											1359
		Chi-sq.	3.0	15.1	13.5	5.5	3.8	21.5	0.8	17.7	80.7***
	Ylg. 10-19	Breed.	51.3	27.8	3.4+	8.1	6.4-	0.4-	0.4	2.1	234
		Post.	49.7	20.4-	0.6-	8.8	13.5	3.8+	2.1+	1.1	889
		Fall	40.9-	31.5+	2.0	9.7	12.6	2.3	0.6-	0.5	660
											1783
		Chi-sq.	7.5	19.1	12.2	0.6	7.7	8.7	8.3	5.1	69.2***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

differences in period frequency of feeding, motionless or upright behaviors tended to have a unique pattern of seasonal frequency.

Calling frequency tended to decrease each period of the season. Among nine groups of males having significant differences in calling frequency during the season, all groups called more frequently during the breeding season than they did during the postbreeding or fall periods of the season.

Two patterns of seasonal frequency were noted for grooming and nest gathering. These patterns were 1) no difference in frequency each period of the year (eight and six groups, respectively), and 2) a peak in frequency during the postbreeding season (eight and 11 groups, respectively).

The most consistent seasonal patterns of moving and encounter frequencies among males was a seasonal low in frequency during the postbreeding period. Significant differences in seasonal frequency of moving were observed among 11 groups of males. Seven of these groups had low frequencies of moving during the postbreeding period. Eleven groups of males having significant differences in the seasonal frequency of encounters conformed to the pattern of a lower frequency during postbreeding than during the breeding and fall periods of the season.

Seasonal organization of behavior among females. The proportion of time spent in eight behaviors by females during the gestation, lactation and postweaning periods was compared for each of 15 groups of females (Table 3). In all cases, females apportioned their time spent in the eight behaviors differently each period of the season

Table 3. Comparisons of the relative frequency of eight behaviors within groups of female Uinta ground squirrels during the gestation, lactation and postweaning periods of the 1965, 1966, 1969 and 1970 seasons. Behavior frequency displayed as percentage.

Year	Group	Period	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
1965	Ad. 0-9	Gest.	54.7-	10.0-	3.9+	6.9	9.5+	7.4+	6.6+	1.0	1227
		Lact.	66.3+	14.7-	2.3-	7.8	3.7-	1.5-	3.1-	0.5-	1527
		Post.	50.0-	17.8+	2.1	10.6	10.6+	3.4	3.0	2.4+	292
											3046
		Chi-sq.	20.8	16.9	6.9	4.2	40.7	58.7	20.2	9.9	178.6***
	Ad. 10-19	Gest.	59.7	12.6	2.5+	8.9	8.0	3.5	3.5	1.1	707
		Lact.	71.2+	8.5-	0.6-	10.8	3.7-	1.8	2.4	1.0	571
		Post.	50.0-	18.4+	0.0	11.8	11.8+	3.9	0.0	3.9	76
											1354
		Chi-sq.	8.5	8.0	8.2	1.5	11.7	3.5	3.7	4.8	50.0***
	Ylg. 0-9	Gest.	63.8	8.9-	3.9	6.5-	8.8	5.2+	2.5	0.5	1057
		Lact.	63.3	11.2	3.2	9.7+	6.3-	1.9-	3.9+	0.5	1335
		Post.	56.3	20.9+	2.4	5.2-	10.7+	2.6	1.6-	0.3	382
											2774
		Chi-sq.	2.8	35.3	2.1	11.3	9.4	20.7	7.1	0.4	89.1***
	Ylg. 10-19	Gest.	56.2	14.8	3.6	6.6	10.7+	4.1+	3.6	0.3	1014
		Lact.	59.8	16.5	2.7	8.6+	5.1-	1.4-	4.8+	1.1+	952
		Post.	68.1+	17.0	1.2	3.0-	9.0	0.3-	1.5-	0.0	335
											2301
		Chi-sq.	6.0	1.3	5.4	11.6	19.2	22.9	7.6	7.2	81.0***
1966	Ad. 0-9	Gest.	54.3	13.9	2.5	6.4	15.8+	4.3+	2.5	0.3-	957
		Lact.	60.4+	15.1	1.9	6.9	8.4-	1.6-	3.8	2.0+	946
		Post.	45.6-	16.4	0.6	8.8	17.0+	6.4+	1.8	3.5-	171
											2074
		Chi-sq.	6.9	0.9	2.8	1.2	24.0	16.6	3.6	16.6	72.7***
	Ad. 10-19	Gest.	56.5+	13.0-	1.6	7.5-	12.8+	5.0+	3.3	0.3-	1932
		Lact.	48.1-	21.3+	1.0-	13.0+	9.0+	1.9-	4.1	1.6+	1427
		Post.	55.2	14.2	2.8+	13.0+	7.7-	2.2	4.9	0.0-	324
											3683
		Chi-sq.	11.2	35.3	6.3	28.2	14.2	24.5	2.7	20.0	143.0***
	Ylg. 10-19	Gest.	57.9+	13.8-	1.5	4.7-	9.6	4.8+	7.5+	0.3-	1633
		Lact.	54.7	21.9+	1.2	6.8	8.4	1.7-	3.3-	2.0+	1284
		Post.	39.4-	23.1+	1.3	18.9+	10.9	2.9	3.2-	0.3	312
											3229
		Chi-sq.	16.3	31.0	0.3	77.5	2.1	20.9	26.6	23.0	197.6***
	Ylg. 20-29	Gest.	56.5+	12.3-	2.6+	5.2-	12.2	5.6+	4.0	0.6	1041
		Lact.	45.9-	21.9+	0.8-	9.8+	13.6	1.9-	4.8+	1.2	734
		Post.	50.2	26.1+	0.7	10.1+	11.1	1.6-	0.0-	0.3	307
											2082
		Chi-sq.	9.6	36.7	10.3	15.3	1.1	19.8	13.9	3.3	110.1***

Table 3. Continued.

Year	Group	Period	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1969	Ad. 10-19	Gest.	55.1	10.6-	1.4	11.4-	13.2+	6.3+	1.4	0.5	555
		Lact.	54.2	17.7	1.9	20.0+	4.2-	1.7-	2.7	2.3+	670
		Post.	55.7	18.4+	3.3	9.8-	10.7	1.6-	0.4	0.0-	244
											1469
		Chi-sq.	0.9	10.7	3.1	17.1	30.9	22.1	5.1	10.7	100.5***
	Ylg. 10-19	Gest.	50.4	14.0	1.1	16.5	10.7+	4.8+	1.8	0.7	272
		Lact.	46.2-	16.6	0.8	24.9+	4.7-	1.7	3.6+	1.5+	530
		Post.	58.6+	14.1	1.6	14.4-	7.9	2.6	0.8-	0.0-	382
											1184
		Chi-sq.	6.7	1.2	1.3	14.2	9.4	6.3	7.9	6.0	53.2***
	Ylg. 20-29	Gest.	47.0	13.1	1.7	19.1	10.3	4.8	1.9	2.1	419
		Lact.	42.9	14.8	3.1+	23.5	8.5	4.8	1.0	1.5	413
		Post.	58.3+	17.4	0.4-	15.8	6.0	1.2-	0.0-	0.8	247
											1079
		Chi-sq.	7.8	1.9	6.2	4.9	3.2	6.2	5.2	1.8	37.3***
1970	Ad. 0-9	Gest.	61.5	13.1	0.8	4.6-	12.4+	4.3	2.0	1.3	605
		Lact.	56.4	14.3	0.5	13.9+	7.4-	3.5	2.2	1.8	1084
		Post.	51.2	20.8+	1.3	7.4-	14.5+	4.8	0.0-	0.2	379
											2068
		Chi-sq.	4.5	10.4	2.2	36.8	18.3	1.0	8.2	4.6	85.9***
	Ad. 10-19	Gest.	57.2	10.7-	2.0+	8.6	13.7+	4.2+	3.2+	0.5	1284
		Lact.	59.0	17.7+	0.6-	11.0	7.3-	1.7-	1.4	1.3	1742
		Post.	56.4	15.4	1.2	10.4	14.2+	1.7	0.0-	0.7	422
											3448
		Chi-sq.	0.6	25.0	13.1	4.5	34.4	19.9	21.1	5.4	124.1***
	Ylg. 10-19	Gest.	57.4	21.7	0.7	6.1-	8.3	2.5	2.2+	1.1	277
		Lact.	49.5	22.2	0.0	13.4+	7.0	1.0	6.1+	0.8	396
		Post.	57.4	22.3	1.1	6.4	7.4	3.2	0.0-	2.1	94
											767
		Chi-sq.	2.3	0.0	3.4	10.0	0.3	3.2	10.5	1.4	31.0**
	Ylg. 20-29	Gest.	55.6	8.8-	2.1	8.7	17.2+	5.0	1.6	1.0	862
		Lact.	57.8	20.0+	1.1	4.9-	7.3-	4.7	2.3+	2.0+	966
		Post.	57.5	15.4	1.8	11.1+	10.7	3.1	0.0-	0.5-	449
											2277
		Chi-sq.	0.4	38.3	2.6	18.4	38.0	2.4	10.1	6.2	116.4***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

($P<.005$). Thus like males, it appears likely that the behavior of female ground squirrels also varies with period of the homeothermic season.

As was the case with males only five general patterns were considered when enumerating consistent patterns of frequency of specific behaviors between periods of the season. These patterns were the same as considered for males. The seasonal patterns of frequencies of specific behaviors among the 15 groups of females were variable (Table 3).

The most consistent seasonal pattern of feeding frequency among the 15 groups of females was no difference in frequency between the three periods of the season (six groups). No consistent pattern of difference was observed among the nine groups of females having significant differences in frequency of feeding during the season.

The most consistent seasonal pattern of encounter frequency among females was no difference between periods of the season (nine groups). However, among five groups of females encounter frequency was lower during the lactation period than during the gestation and postweaning periods.

Among 10 groups of females having a significant difference in the frequency of moving between periods of the season, seven groups had higher frequencies of moving during the lactation period than during the gestation or postweaning periods.

Patterns of grooming frequency during the season were more or less evenly divided between no differences (four groups), a progressive decrease as the season advanced (five groups) and a seasonal low during the lactation period (six groups).

Among 11 groups of females having significant differences in the seasonal frequency of motionless behavior, 10 groups were motionless less often during the lactation period than during the gestation or postweaning periods.

Two patterns of seasonal frequency were noted for upright, nest gathering and calling behavior among females. These patterns were 1) no difference in frequency each period (5, 4, and 7 groups, respectively), and 2) a peak in frequency during the lactation period (7, 6 and 7 groups, respectively).

The manner in which males and females apportioned their behavior within a season appears to be fundamentally related to the seasonal partitioning of reproductive events. High frequencies of calling, encounters and moving by breeding males corresponds with the aggressive, exploratory nature of sexually motivated males (Balph and Balph 1966, Burns 1968). The high frequencies of moving and of encounters by males during the fall corresponds with the fall increase in androgen synthesis (Ellis and Balph 1976) and the accompanying increase in sexual behavior (Slade and Balph 1974). The high frequencies of grooming and nest gathering during the midperiod of the season may be the result of low social interaction levels of males during the period. During periods of low social and sexual interaction more time can be devoted to maintenance behavior.

The high frequencies of moving, upright, nest gathering and calling by lactating females are probably a result of the metabolic demands of lactation and maternal behavior. Given the sudden increase in metabolic requirements of lactation (Myrcha et al. 1969), the increase in home range size (Ruff 1971) and the need for frequent

feeding of the young, an increase in the frequency of moving is likely. With increased movement, increased alert behavior (upright) is likely. The threshold necessary to elicit calls by females is low during the lactation period (Balph and Balph 1966). Thus, the high frequency of calling during the lactation period should be expected. The presence of young in the nest probably requires increased maintenance and upkeep of the nest, hence, increased frequency of nest gathering. Among female laboratory mice (Mus spp.), postpartum nest gathering was significantly higher than during gestation (Levenson and Wilsoncroft 1974). The low frequency of motionless behavior during lactation is probably due to the high metabolic demands of lactation, forcing greater activity. I cannot explain the low rates of grooming observed during lactation in this study. It would seem likely that the process of lactation would contribute to high frequencies of grooming.

In general, it does appear that ground squirrels organize their behavior with regard to period of the season. Given that this species lives in an environmental characterized by seasonal fluctuations of resources and thermal conditions, a discrete seasonal partitioning of behavior and reproductive events would likely contribute to relative fitness of the individual.

Comparisons of behavior by males and females during periods of the day. To assess the diurnal organization of behavior by ground squirrels, I compared the behavior of a group of animals during five times of the day (Tables 4 and 5). Because of the possible influence of seasonal period upon behavior frequency (Tables 2 and 3), the data was segregated into periods of the season. The time periods

Table 4. Comparisons of the relative frequency of eight behaviors within groups of male Uinta ground squirrels during five periods of the day during different periods of the 1965, 1966 and 1970 seasons. Behavior frequency displayed as percentage.

Group	Seasonal Period	Period Of Day	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1965 Ad. 0-9	Breed.	1	55.8+	29.8-	2.8	1.7	6.1	0.0	0.0	3.9	238
		2	27.2-	50.3+	5.3	4.1	7.7	1.2	0.0	4.1	223
		3	33.7	38.3	5.1	5.6	8.7	2.0	0.0	6.6	258
		4	33.1	46.6	2.5	3.7	8.0	1.2	0.0	4.9	214
		5	43.8	38.4	3.6	1.8	0.9	0.9	0.0	10.7	147
											1080
		Chi-sq.	22.9	10.9	3.1	5.4	7.5	3.7	0.0	7.2	60.6***
	Post.	1	57.6	21.6	0.8	5.1-	7.9	4.1	2.0-	1.0	291
		2	43.2-	32.0+	1.0	8.7	6.8	2.9	4.4	1.0	152
		3	31.9-	27.7	1.1	16.0+	11.7+	3.2	8.5+	0.0	70
		4	47.4	19.6	3.1	9.8	7.7	2.6	7.2+	2.6	144
		5	72.3+	17.5	0.7	5.8	1.5-	1.5	0.7-	0.0	101
											758
		Chi-sq.	24.1	11.1	6.4	13.7	9.4	2.5	17.8	6.6	91.6***
1966 Ad. 0-9	Breed.	1	49.7+	28.2	1.7	6.4-	10.2	2.5	0.0	1.3	397
		2	32.5-	34.4	3.7	8.0	15.5+	1.9	0.0	4.0	272
		3	32.7-	36.8	4.1	10.8	10.8	1.6	0.0	3.2	266
		4	35.4	33.3	4.4	12.6+	9.1	2.3	0.0	2.9	287
		5	38.6	33.6	4.7	9.2	7.1-	4.7	0.0	2.0	249
											1471
		Chi-sq.	21.7	4.9	6.7	9.7	11.5	7.3	0.0	6.7	68.5***
	Post.	1	49.6	23.7	1.8	6.6	9.6	6.6	2.2-	0.0	219
		2	45.3	23.3	0.0	4.7	5.8	8.1	12.8+	0.0	81
		3	33.3	30.9	1.2	3.7	12.3	7.4	11.1	0.0	75
		4	30.7-	20.0	0.0	12.0	16.0	6.7	14.7+	0.0	78
		5	56.1	21.4	1.0	3.1	9.2	2.0	7.1	0.0	91
											544
		Chi-sq.	9.6	2.4	2.8	7.0	4.6	3.5	18.2	0.0	48.1**
1966 Ad. 10-19	Breed.	1	40.6	29.9	2.8-	7.0	9.3	5.1	2.8	2.3	191
		2	40.7	24.0	10.7+	3.3	8.7	10.0+	1.3	1.3	134
		3	27.7	37.4	7.7	10.3	11.0	2.6	1.3	1.9	138
		4	28.4	34.7	4.5	8.0	13.1	2.8	3.4	5.1	157
		5	35.1	40.3	5.8	8.4	4.2	1.0-	1.6	3.7	170
											790
		Chi-sq.	7.9	8.3	10.5	5.5	8.7	18.8	3.0	5.3	68.1***
	Post.	1	52.6	19.9	1.9	7.6	10.4	5.6	1.9	0.0	211
		2	45.3	18.7	0.0	10.7	16.0	4.0	5.3	0.0	75
		3	31.0	18.3	1.4	9.8	19.7	7.0	12.8+	0.0	71
		4	39.1	20.7	0.0	14.1	19.6	4.3	2.2	0.0	92
		5	56.2	18.0	1.1	5.6	15.7	2.2	1.1	0.0	82
											531
		Chi-sq.	8.1	0.3	3.1	4.5	5.4	2.4	19.9	0.0	43.7**

Table 4. Continued.

Group	Seasonal Period	Period Of Day	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1966 Ylg. 20-29	Breed.	1	60.2	14.5-	1.6	2.7	15.6	4.3	0.0	1.1	186
		2	40.7	33.0+	5.5	4.4	14.9	2.2	0.0	0.0	91
		3	42.2	34.4+	4.7	6.3	4.7	3.1	0.0	4.7	64
		4	58.5	20.0	1.5	3.1	13.8	0.0	0.0	3.1	65
		5	58.1	19.8-	3.5	7.0	8.1	7.2	0.0	2.3	86
											492
		Chi-sq.	8.0	20.9	4.2	4.1	5.5	4.2	0.0	5.8	52.7***
	Post.	1	53.8+	19.1	0.9	7.6	8.0	6.7	2.7	1.3	225
		2	35.9	28.2	0.8	8.5	10.3	12.0+	4.3	0.0	117
		3	25.2-	33.6	0.0	11.8	18.5+	5.8	3.4	1.7	119
		4	45.3	26.7	0.0	9.3	9.3	4.0	2.7	2.7	75
		5	50.4	26.4	1.7	11.6	7.4	0.8-	0.0	1.7	121
											657
		Chi-sq.	17.4	7.1	2.8	2.2	9.9	12.8	4.7	2.7	59.6***
	Fall	1	52.3+	26.5	1.5	2.7-	12.1	3.8	1.1	0.0	293
		2	33.9	40.5	3.3	3.3	14.8	0.8	3.3	0.0	134
		3	30.4-	27.0	3.5	12.0+	26.1+	0.0	0.9	0.0	127
		4	25.4-	37.3	0.0	16.4+	17.9	3.0	0.0	0.0	74
		5	42.9	27.3	5.2	9.1	10.3	5.2	0.0	0.0	86
											714
		Chi-sq.	16.9	7.1	5.7	23.9	11.8	7.8	6.1	0.0	79.3***
1970 Ad. 0-9	Breed.	1	47.3	23.5	2.7	9.8	15.0	1.6	0.0	0.0	268
		2	36.3-	24.2	2.3	16.3+	19.1	1.9	0.0	0.0	157
		3	35.3-	28.4+	3.9	14.4+	15.7	2.3	0.0	0.0	224
		4	54.0+	21.3	2.7	8.2-	11.7	2.1	0.0	0.0	319
		5	61.2+	14.5-	2.8	9.8	10.3	1.4	0.0	0.0	157
											1125
		Chi-sq.	27.8	11.5	1.4	12.1	8.6	0.7	0.0	0.0	62.1***
	Post.	1	62.9+	12.9-	0.5	7.0-	9.0	6.2+	0.0-	1.5	475
		2	41.3-	23.0+	2.9+	13.0	9.6	3.8	3.8+	2.4	255
		3	41.2-	21.5	1.1	18.6+	11.3	1.7	3.4+	1.1	217
		4	47.3	21.3	3.2+	11.2	13.3	1.1-	0.5	2.1	230
		5	60.0	15.2	0.0	15.9	6.9	1.4	0.0	0.7	178
											1355
		Chi-sq.	19.7	11.6	11.5	17.0	4.2	14.7	23.1	2.1	103.9***
	Fall	1	61.1+	14.3-	1.5	4.9-	12.8	5.4	0.0	0.0	203
		2	30.6-	37.8+	5.4	10.8	14.4	0.9	0.0	0.0	111
		3	25.4-	30.5	1.7	20.3-	18.6	3.4	0.0	0.0	59
		4	36.4	27.3	3.9	7.7	16.9	7.8	0.0	0.0	77
		5	55.2	18.4	1.1	14.9	9.2	1.1	0.0	0.0	87
											537
		Chi-sq.	24.1	19.7	5.7	14.3	3.0	8.5	0.0	0.0	75.4***
1970 Ylg. 10-19	Post.	1	54.7	18.9	0.5	5.3	14.7	4.2	1.1	0.5	229
		2	36.4-	24.8	0.6	9.7	17.0	7.3	3.0	1.2	199
		3	41.2	23.5	0.8	11.8	17.6	4.2	0.0	0.8	143
		4	44.7	18.7	0.0	13.8	13.8	4.9	3.3	0.8	148
		5	60.7+	15.0	1.4	9.3	9.3	2.9	0.7	0.7	169
											888
		Chi-sq.	13.2	4.4	1.8	6.6	4.0	3.4	7.0	0.5	40.9
	Fall	1	52.5	22.2-	1.5	4.4	15.6	3.7	0.0	0.0	198
		2	31.7-	45.5+	1.0	7.9	10.9	3.0	0.0	0.0	148
		3	30.6-	43.5+	0.0	8.1	16.1	1.6	0.0	0.0	91
		4	44.4	31.9	1.4	5.6	15.3	1.4	0.0	0.0	106
		5	60.8+	20.3-	2.7	8.1	6.8	1.4	0.0	0.0	109
											652
		Chi-sq.	12.7	15.7	2.0	1.8	4.0	1.8	0.0	0.0	38.0

* = significant at .05.
** = significant at .01.
*** = significant at .005.

Table 5. Comparisons of the relative frequency of eight behaviors within groups of female Uinta ground squirrels during five periods of the day during different periods of the 1965, 1966 and 1970 seasons. Behavior frequency displayed as percentage.

Group	Seasonal Period	Period of Day	Behavior								
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1965 Ad. 0-9	Gest.	1	58.3	7.9	3.9	7.3	12.4	8.8	1.2-	0.3	331
		2	47.6	14.7	4.3	6.0	9.1	10.8+	7.4	0.0	231
		3	43.2-	11.2	5.2	8.4	12.0	8.8	9.2+	2.0+	250
		4	62.5+	9.1	0.4	6.5	7.6	5.5	4.0	0.7	275
		5	67.6+	11.8	0.7	6.6	5.9	0.0-	5.1	2.2+	136
											1223
		Chi-sq.	16.0	6.9	4.7	1.1	7.0	16.5	21.2	9.4	82.8***
	Lact.	1	59.6	15.5	4.0	8.6	5.0	2.7	3.6	1.5+	529
		2	60.3	17.9	2.1	9.4	2.9	1.5	5.9+	0.0-	376
		3	58.9	20.5	3.6	8.9	4.5	0.9	2.7	0.0	123
		4	64.9	16.5	2.5	9.0	4.7	1.4	0.7-	0.4	309
		5	74.3	13.5	1.8	6.4	2.9	0.6	0.6-	0.0	188
											1525
		Chi-sq.	5.4	2.8	3.8	1.2	2.9	4.7	17.4	10.3	48.5**
1965 Ylg. 0-9	Gest.	1	62.8	10.8	3.9	7.6	9.1	5.4	0.3-	0.3	334
		2	60.5	10.2	4.5	4.5	7.3	8.5+	3.4	1.1	179
		3	50.3-	11.5	3.6	10.9	12.7	6.1	3.6+	1.2	166
		4	65.6	6.6	5.2	5.2	11.9	3.1	2.2	0.0	229
		5	85.8	4.7	4.1	4.1	2.0-	1.4-	0.7	0.0	149
											1057
		Chi-sq.	15.5	7.0	3.8	8.5	13.3	10.7	11.0	0.0	69.7***
	Lact.	1	68.1	9.5	3.8	7.0-	6.1	2.3	2.9	0.3	614
		2	54.7	11.7	2.2	13.4	6.1	0.0	10.1+	1.1	179
		3	52.4-	15.9	2.8	13.1	6.9	2.8	5.5	0.7	145
		4	56.7	13.9	2.7	15.0+	5.9	2.8	2.8	0.5	189
		5	73.9+	9.7	3.4	7.2	3.4	1.0	1.0-	0.5	208
											1335
		Chi-sq.	11.6	6.1	1.4	15.4	2.5	6.0	25.7	1.7	70.5***
1965 Ylg. 10-19	Gest.	1	59.2	12.7	3.3	7.6	10.6	3.9	2.7	0.0	331
		2	43.8-	19.5	2.4	7.1	15.4+	7.7+	3.6	0.6	169
		3	46.2	24.2+	5.3	3.8	15.2	0.8-	4.5	0.0	132
		4	53.4	11.6	3.4	8.1	12.0	6.3	5.3	0.0	208
		5	75.1+	11.8	3.6	4.7	1.8-	1.2-	1.2	0.6	169
											1009
		Chi-sq.	18.5	13.8	1.9	3.7	18.6	14.6	5.6	4.0	80.8***
	Lact.	1	70.1+	11.6-	4.0	6.7	3.4	1.8	0.9-	1.5	390
		2	53.0	18.2	2.2	7.7	5.5	0.6	10.5+	2.2	215
		3	28.7-	33.3+	3.4	20.6+	4.6	2.3	6.9	0.0	103
		4	58.7	15.9	3.2	7.9	8.7	2.4	3.2	0.0	150
		5	74.7+	11.4	1.3	7.6	2.5	0.0	1.3	1.3	94
											952
		Chi-sq.	23.9	21.8	2.1	16.2	6.6	3.5	29.5	4.2	107.9***
1966 Ad. 0-9	Gest.	1	57.4	11.9	3.7	5.4	13.1-	5.7	2.8	0.0	311
		2	38.9-	16.6	1.3	9.6	27.4+	3.8	1.3	1.3	139
		3	43.3-	16.4	1.2	8.2	24.0+	2.9	4.1	0.0	150
		4	44.5	16.7	2.9	7.2	19.6	5.7	2.9	0.5	185
		5	70.8+	12.8	1.0	5.6	8.7-	0.5-	0.5	0.0	172
											957
			24.9	3.6	6.3	3.7	26.2	10.3	6.2	7.9	89.2***

Table 5. Continued.

Group	Seasonal Period	Period of Day	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
	Lact.	1	66.8	13.4	2.0	5.9	4.9	1.0	4.2	2.0	382
		2	62.4	14.5	0.0	6.0	8.5	1.7	6.0	0.9	145
		3	67.5	14.5	1.2	6.0	8.4	0.0	2.4	0.0	103
		4	52.9	18.5	1.9	7.4	13.0	5.6+	1.9	0.0	134
		5	61.6	11.6	4.8	7.5	7.5	1.4	4.1	1.4	182
											946
		Chi-sq.	3.1	2.3	7.9	0.6	7.4	11.8	3.0	4.0	40.1
1966 Ad. 10-19	Gest.	1	60.8+	11.5	1.2	7.2	10.7-	6.4+	2.1-	0.1	707
		2	44.1-	16.1	1.2	6.1	21.9+	3.6	6.7+	0.3	310
		3	49.2	14.4	1.9	4.9	18.6+	3.0	7.1+	0.8	249
		4	49.8	15.8	2.3	6.9	16.5	4.3	3.6	0.7	286
		5	66.1+	13.1	1.7	8.4	8.2-	1.5-	0.7-	0.2	380
		Chi-sq.	23.0	5.4	2.2	3.2	36.0	16.7	33.0	3.3	122.8***
	Lact.	1	58.8	15.0	1.0	12.1	6.4	1.6	4.5	0.6-	595
		2	50.3	20.7	1.8	9.5	10.7	1.2	3.6	2.4	206
		3	44.9	19.6	1.3	13.9	8.9	0.6	5.7	5.1+	193
		4	47.0	19.5	6.1+	10.9	9.1	2.4	4.3	0.6	200
		5	52.9	21.1	0.5	8.4	9.9	1.0	1.0	2.1	233
											1427
		Chi-sq.	6.4	7.2	20.5	3.2	4.2	2.2	5.8	15.6	65.1***
1966 Ylg. 20-29	Gest.	1	58.8	13.4	2.6	2.6-	11.5	8.0	2.9	0.1	313
		2	49.3	13.1	2.5	5.6	14.4	10.0+	4.4	0.0	160
		3	52.1	13.2	4.2	7.6	11.8	4.9	5.5	0.1	144
		4	55.6	7.9	1.7	8.4+	19.1	1.7-	5.1	0.0	178
		5	60.4	13.6	2.6	4.3	11.5	3.4	3.4	0.0	235
											1030
		Chi-sq.	2.9	3.6	1.9	10.0	6.2	15.4	2.6	0.7	43.3*
	Lact.	1	58.2+	17.8	1.0	5.3	11.1	1.4	3.8	1.4	208
		2	45.3	20.3	0.8	11.7	10.9	2.3	7.8	0.8	128
		3	44.7	27.2	1.9	8.9	10.7	1.9	4.9	0.0	103
		4	25.6-	30.6+	0.0	9.9	23.1+	2.5	6.6	1.7	121
		5	47.1	14.8-	0.6	14.8	14.8	1.9	4.5	1.3	155
											715
		Chi-sq.	17.7	10.9	2.6	8.9	10.4	0.5	3.0	1.8	55.9***
1970 Ad. 0-9	Gest.	1	54.7	18.0+	0.0	5.8	12.2	5.8	1.4	2.2	139
		2	42.6-	10.3	1.5	5.9	20.6+	11.8+	4.4	2.9	68
		3	58.6	14.7	0.0	5.2	15.5	1.7	2.6	1.7	116
		4	63.9	9.8	2.5	6.6	10.7	4.1	2.5	0.0	122
		5	85.0+	4.4-	0.0	4.4	5.3-	0.0-	0.0	0.9	113
											558
		Chi-sq.	15.2	11.0	8.3	0.5	9.6	16.8	4.9	3.6	70.0***
	Lact.	1	77.1+	7.6-	0.3	5.1-	4.5	4.0	0.8	0.6	353
		2	39.1-	21.0+	0.0	20.3+	8.0	4.3	5.1+	2.2	138
		3	44.3-	17.0	1.9	18.9+	7.5	2.8	4.7+	2.8	106
		4	54.6	12.5	0.0	18.4+	6.6	3.3	2.6	2.0	152
		5	70.4	10.2	0.9	10.6	5.1	0.0	0.0-	2.8	216
											965
		Chi-sq.	33.0	17.8	6.4	31.3	3.0	8.7	17.7	5.0	122.9***
	Post.	1	56.5	10.7-	0.6	5.6-	19.8	5.6	0.6	0.6	177
		2	39.0	31.7+	1.2	6.1	11.0	9.8+	1.2	0.0	82
		3	36.0	29.3+	2.7	17.3+	10.7	1.3	0.0	2.7	75
		4	47.7	16.9	0.0	20.0+	10.8	3.1	1.5	0.0	65
		5	59.3	14.0	1.2	10.5	14.0	1.2	0.0	0.0	86
											485
		Chi-sq.	8.0	19.2	3.0	14.7	5.4	9.6	2.4	6.5	68.9***

Table 5. Continued.

Group	Seasonal Period	Period of Day	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
1970		1	56.2	11.8	2.6	9.5	13.3	5.6+	0.8-	0.3	390
Ad. 10-19		2	46.2-	11.8	0.4	9.7	24.4+	3.8	3.8	0.0	238
		3	53.4	11.5	1.3	9.8	15.8	5.6	2.1	0.4	234
		4	61.6	9.8	2.6	7.5	10.4-	2.3	4.9+	1.0	307
		5	67.0+	7.3	2.8	5.6	12.3	1.1-	3.9	0.0	179
											1348
		Chi-sq.	9.7	3.1	5.3	3.4	20.0	10.2	12.0	4.7	68.6***
	Lact.	1	65.1	13.1	0.6	10.4	6.3	3.2+	0.3-	0.9	527
		2	50.5-	23.2+	1.4	9.5	8.6	0.9	4.5+	1.8	220
		3	54.1	23.8+	0.0	7.6	11.6	0.0	1.2	1.7	172
		4	58.9	18.1	0.3	12.9	8.9	0.0-	0.6	0.3	326
		5	75.8+	12.5-	0.0	7.3	4.4	0.0-	0.0-	0.0	248
											1493
		Chi-sq.	15.4	17.8	3.5	5.8	9.3	25.5	30.4	7.2	114.9***
1970	Post.	1	60.1+	12.3-	1.6	9.9	10.7	3.7	0.0-	1.6	243
Ylg. 20-29		2	48.0	22.4	0.0	14.4	9.6	3.2	1.6	0.8	125
		3	43.1	25.5+	1.0	11.8	13.7	2.9	2.0	0.0	102
		4	31.3-	24.0	3.1	17.7	10.4	0.0	5.2+	8.3+	96
		5	57.5	14.2	0.9	13.2	12.3	0.9	0.0	0.9	106
											672
		Chi-sq.	13.7	11.5	4.4	3.8	1.1	5.1	15.8	22.0	77.3***
	Gest.	1	58.1	9.7	1.6	7.0	16.3	6.2	0.0-	1.2	258
		2	39.0-	14.9	2.8	15.6+	18.4	6.4	2.8	0.0	141
		3	49.1	12.9	1.8	8.2	19.9	4.1	2.9	1.2	171
		4	54.5	11.4	1.7	6.8	15.9	3.4	4.5+	1.7	176
		5	73.7+	5.8	4.3	5.1	9.5	1.5	0.0-	0.0	137
											883
		Chi-sq.	16.8	6.3	3.9	11.8	5.7	6.1	15.4	4.1	70.0***
	Lact.	1	65.9+	14.9	0.8	3.4-	6.1	6.5+	0.8	1.5	261
		2	45.2-	21.9	0.7	14.4+	10.3	3.4	2.7	1.4	146
		3	46.7-	28.3	1.3	11.8	6.6	2.0	0.7	2.6	152
		4	61.7	19.5	1.3	8.1	4.0	2.7	1.3	1.3	149
		5	66.7	17.1	0.9	7.2	7.2	0.0-	0.0	0.9	111
											819
		Chi-sq.	12.1	9.4	0.6	16.4	4.5	11.8	5.4	1.5	61.7***
	Post.	1	62.0	11.6	2.3	6.9-	8.8	8.3+	0.0-	0.0	216
		2	52.4	16.9	3.2	6.5	10.5	6.5	3.2	0.8	124
		3	38.7	29.0+	1.0	17.2+	6.5	0.0-	5.4+	2.2	93
		4	51.6	11.6	0.0	24.2+	9.5	0.0-	2.1	1.1	95
		5	65.0	12.5	0.0	2.5-	13.8	2.5	0.0	3.8	80
											608
		Chi-sq.	8.2	14.7	5.5	30.3	2.7	16.9	13.3	8.1	99.8***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

considered were the first and last two hours of the diurnal period and three equivalent midday periods representing late morning, noonday and early afternoon. Only those groups of animals for which I had approximately 500 or more observations during two consecutive seasonal periods were used. The proportion of time spent in the eight behaviors by squirrels during periods of the day was different ($P<.10$) in 12 of 14 comparisons for males and in 20 of 21 comparisons for females.

Five basic patterns of diurnal frequency of specific behaviors were considered. These were 1) no differences in hourly frequency throughout the day, 2) high frequencies in the first and last two hours of the day, 3) a decreasing frequency from morning to evening, 4) an increasing frequency from morning to evening, and 5) a peak in frequency during the hours bounded by the first and last two hours of the day.

The primary pattern of diurnal feeding frequencies among squirrels during all periods of the season was a lower frequency of feeding during the late morning, noonday and early afternoon periods than during the first and last two hours of the day (Tables 4 and 5). This pattern was observed among 27 of 35 male and female comparison sets.

The consistent pattern of encounter and calling frequencies during hours of the day was no difference in frequency between periods of the day. Thirty-two of 35 sets of comparisons showed no differences in encounter frequency during periods of the day and 25 of 29 sets of comparisons showed no differences in calling frequency during periods of the day.

Two patterns of diurnal frequency were noted for moving, upright, motionless, grooming and nest gathering behaviors. These patterns were 1) no difference in frequency between periods of the day (19, 21, 24, 19 and 10 sets of comparisons, respectively), and 2) a higher frequency during late morning, noonday and early afternoon than during the first and last two hours of the day (15, 14, 11, 13 and 11 sets of comparisons, respectively). There were only 21 sets of comparisons having observations of nest gathering. The remaining behaviors were all observed in 35 sets of comparisons each.

The most dominant behavior of ground squirrels is feeding. Given that these animals are only active about 90 days a year and do not cache food, the dominance of feeding is not surprising. High frequencies of feeding during the first two hours of the day should be expected since the animal presumably emerges with an empty or near empty gut. Any of the nutrient depletion-repletion hypotheses (Marler and Hamilton 1966, Walker and Remley 1970 and others) would be appropriate explanations of intense morning feeding with a subsequent decrease in feeding during the following time intervals. However, if the frequency of feeding is regulated by physiological signals of nutrient depletion-repletion or by the rate of gastric clearing then it becomes difficult to explain the high rates of feeding during the last two hours of the day. Other investigators suggest feeding to be regulated by either endogenous circadian signals of body nutrient depletion-repletion rather than the short term consequences of recently ingested food (Panksepp 1973) or as

the result of a circadian influence on gastric clearing (Davies 1977). However, Collier et al. (1972), Marler and Hamilton (1966), and Panksepp and Krost (1975) argue that environmental variables may provide more proximate constraints over feeding patterns than physiological factors. One environmental factor that may contribute to the high frequencies of feeding during morning and evening is water content of the plant material and/or amount of moisture on the plant. Humidity of the study site followed a cyclic pattern similar to the pattern of feeding. An alternative hypothesis to high frequency of feeding during the last two hours is that it is a behavioral response in anticipation of a long period without food.

Qualitative evidence suggests that feeding by ground squirrels during the morning and evening hours occurs within the core areas of their home ranges. As the core areas of ground squirrels are usually segregated from one another (Ruff 1971), animals are able to feed with little social interference.

The high frequency of moving, upright and nest gathering during the late morning, noonday and early afternoon is likely influenced by a number of different factors. Some that would seem advantageous would be a need for the assessment of the environment, novel stimuli seeking, a need for social interaction and maintenance of the home range (Brown 1966, Brown and Orians 1970). Concomitant with moving is the entrance into less familiar areas of the home range. Thus the increase in frequency of upright and motionless behavior may be a response of the animal becoming more apprehensive as it moves

into more unfamiliar areas. Alternatively, the increase may be responses that facilitate assessment of unfamiliar environments. The increase in nest gathering may simply be a need for nest maintenance following 10-14 hours in the nest. However, the increase in frequency may also be influenced by the daily cycle of dryness of the nest material. During late morning through late afternoon the dead grasses are dryer and perhaps more suitable as nest material.

In conclusion, the daily patterns of behavior appear to be related fundamentally to a cycle of nutritive requirements. Given that all the activities necessary for individual and population survival must be completed in approximately 90 days, the dominance of feeding in the behavioral repertoire is not unexpected. Additionally the partitioning of feeding into two time intervals within the core areas of their home ranges facilitates feeding with little disturbance. Coping with the requirements of living in a social system whose organization is structured by aggressive behavior is more or less restricted to the middle three time intervals of the day.

Comparisons of the behavior of males and females. The influence of the animal's sex upon frequency of behavior was assessed during comparable periods of the season (Table 6). No segregation as to age or date of emergence from hibernation was imposed upon these comparisons. The comparisons made were between the behavior frequencies of all males and all females for seasonal periods of high population density years and low population density years.

The manner in which males and females apportioned their time in the eight behaviors during similar periods of the season was different

Table 6. Comparisons of the relative frequencies of eight behaviors of male and female Uinta ground squirrels during comparable periods of the seasons of high population density years (1965 and 1966) and of the low population density years (1969 and 1970). Behavior frequency displayed as percentage.

Pop. Density	Period	Sex	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
High	Breed./ Gest.	Male	42.3-	31.7+	3.6+	6.4	9.5-	2.4-	1.3-	2.8+	5357
		Female	56.9+	12.3-	2.6-	6.8	11.6+	5.1+	4.0+	0.6-	9304
											14861
		Chi-sq.	142.0	671.2	9.8	0.9	14.8	58.0	83.2	119.1	11099.1***
	Post./ Lact.	Male	48.8-	21.2+	1.7	6.9-	10.3+	4.9+	5.4+	0.8-	4467
		Female	58.4+	16.8-	1.8	9.1+	7.2-	1.7-	3.8-	1.2	8712
											13179
		Chi-sq.	48.9	30.9	0.5	17.2-	34.8	108.8	18.4	4.3	263.8***
	Fall./ Post.	Male	46.7-	27.5+	2.3	5.2-	14.8+	2.3	1.0-	0.2-	2047
		Female	52.8+	19.5-	1.6	10.0+	10.6-	2.5	2.2+	0.9+	2199
											4246
		Chi-sq.	8.0	28.7	3.1	29.9	14.5	0.3	9.3	7.2	101.0***
Low	Breed./ Gest.	Male	47.8-	20.7+	3.4+	10.9	12.1	1.7-	1.0	2.4+	2599
		Female	55.8+	11.8-	1.6-	9.8	13.3	4.6+	2.2+	0.1-	4274
											6873
		Chi-sq.	19.4	84.6	23.0	2.1	1.8	36.7	14.3	22.9	207.7***

Table 6. Continued.

Pop. Density	Period	Sex	Behavior								
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
	Post./ Lact.	Male	50.9-	18.6	0.8	13.0	9.6+	3.9+	1.9	1.3	4482
		Female	54.5+	17.4	1.0	13.8	6.8-	2.7-	2.3	1.6	5801
											10283
		Chi-sq.	6.0	2.0	0.5	1.3	24.4	12.0	1.7	1.7	49.8***
	Fall./ Post.	Male	51.1-	22.0+	2.6+	10.3	11.1	2.1	0.5	0.4	2941
		Female	56.3+	17.0-	1.5-	11.1	10.9	2.6	0.2	0.5	2217
											5158
		Chi-sq.	6.4	16.2	6.2	0.7	0.0	1.6	3.2	0.0	34.3***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

in all comparisons ($P<.005$). However, the magnitude of these differences decreased with each period of the season. Thus it would appear that sex of the individual is an important factor influencing behavior frequency but at a decreasing degree of importance as the season progresses.

Consistent patterns of differences in frequency of specific behaviors between males and females were observed only for feeding and moving. In all six comparisons females led more frequently than did males. The opposite pattern was observed for moving. In five of six comparisons males moved more frequently than did females.

Among the remaining behaviors, differences in frequency of specific behaviors between males and females were most common during the breeding/gestation period. Males had higher frequencies of encounters and calling than did females. Conversely females had higher frequencies of nest gathering during breeding/gestation than did males.

Patterns of grooming frequency between males and females were observed, but during each period the pattern was different. During the breeding/gestation periods females groomed more than males, but during the postbreeding/lactation periods males groomed more than females. During the fall/postweaning period there were no differences in frequencies of grooming between males and females.

The primary pattern of upright behavior was no difference in frequency between males and females (four of six comparisons). A consistent difference in motionless frequency occurred during the postbreeding/lactation periods, with males having a higher frequency than females (two of two comparisons).

The observed differences in frequencies of feeding and moving between males and females can be associated with differences in energetic requirements and functional roles each sex plays throughout the season. Breeding males normally emerge from hibernation weighing in excess of 300 grams (Knopf and Balph 1977). Weight loss for 15 to 30 days following emergence is common. It is therefore likely that breeding males rely on catabolism of body fats to supplement ingested energy. Thus, males can allocate the time normally spent in feeding to those behaviors which enhance breeding success. Concomitantly, the energetic requirements of pregnant and lactating females demand high rates of food intake (Miller 1975, Randolph et al. 1977). Thus the combination of high energetic requirements of gestation among females and the accent on behaviors which contribute to breeding success among males, are the possible causal factors of differential feeding frequencies between males and females during the breeding/gestation period. During postbreeding/lactation males gain weight at an approximate rate of 10 gm per day (Balph, personal communication), but the weights of females are stable. The stable weights of females during this period are presumably due to the high energetic demands of lactation. This difference probably contributes to higher feeding frequencies of females compared to males during the postbreeding/lactation periods. During the fall/postweaning periods males are again sexually active and allocate less time to feeding. Their weights become stable or they begin to lose weight. Conversely, females are gaining weight preparatory to aestivation-hibernation. The higher frequencies

of feeding by females during this period are likely the result of prehibernation fat deposition requirements among females.

The higher frequency of moving by males relative to females is probably related to the difference in sexual activity of the two sexes. Females usually are bred one to three days after spring emergence in or near the hibernation burrow system. After that females are intolerant of conspecifics. Since females emerge over an interval of 30-50 days and are dispersed within the study area, males must move about the area if they are to breed. In the fall period, sexual and aggressive encounters are directed primarily toward juveniles who are also dispersed.

In addition to the differences in feeding and moving, consistent differences were also observed for encounters, grooming, nest gathering and calling between males and females during the breeding/gestation periods. Among breeding males, high frequencies of moving, encounters, and calling should to advantageous in locating receptive females and in spacing conspecifics. Among gestating females, high frequencies of feeding, grooming and nest gathering should contribute to health of the individual and to high productivity.

The principal conclusion of the comparisons of the behavior of male and female ground squirrels is that behavior was correlated with the functional roles each sex plays during periods of the year. Success in fulfilling the roles of a female can be measured by her ability to produce young capable of surviving after weaning without injury to herself and then depositing enough fat to enhance over-hibernation survival. An emphasis by females on maintenance-productivity behaviors (feeding, grooming and nest gathering) should

increase the chances of successfully fulfilling these roles. Success in fulfilling the roles of a male can be measured by how many females he breeds and his ability to deposit enough fat to survive aestivation-hibernation and supplement the low energy intake during the following breeding season. An emphasis by males on those behaviors which contribute to these measures (moving, encounters, and calling during the breeding season and increased feeding during postbreeding) should increase the chances of successfully fulfilling these roles.

Comparisons of the behavior of adults and yearlings. To assess the association between age and behavior frequencies, I tested for the difference between behavior frequency of adults and yearlings of the same sex during similar periods of the year (Tables 7 and 8). Comparisons were made between the behaviors of all adults and all yearlings of the same sex during seasonal periods of high population density years (1965 and 1966) and during seasonal periods of the low density years (1969 and 1970). The manner in which adults and yearlings of the same sex apportioned their time in the eight behaviors during similar periods of the season was different ($P<.10$) in all comparisons. Thus, it would appear that age is a factor influencing behavior frequency of a squirrel.

Although chi-square analysis showed that adults and yearlings of the same sex apportioned their behavior during similar periods differently, there was a lack of consistent patterns of differences in frequency of specific behaviors between age groups during all periods of the season. There was only one instance of a consistent

Table 7. Comparisons of the relative frequencies of eight behaviors of adult and yearling male Uinta ground squirrels during the breeding, post breeding and fall periods during high population density years (1965 and 1966) and of low population density years (1969 and 1970). Behavior frequency displayed as percentage.

			Behavior								
Years	Period	Age	Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
1965-1966	Breed.	Adult	38.9-	35.2+	3.6	7.2+	9.0	2.0-	0.7	3.4+	3346
		Ylg.	48.6+	26.3-	3.6	5.2-	10.4	3.3+	0.8	1.9-	1980
											5326
		Chi-sq.	27.7	31.0	0.0	8.3	2.3	8.7	0.1	10.1	88.2***
	Post.	Adult	52.0+	20.5	1.3	7.8	7.9-	4.5	5.6	0.4-	1817
		Ylg.	46.6	21.7	1.9	6.3	11.9+	5.2	5.3	1.1+	2650
											4467
		Chi-sq.	6.5	0.7	2.3	3.1	16.5	0.9	0.1	5.6	35.7***
	Fall.	Adult	49.5	27.9	3.1	4.8	11.9-	2.8	0.0-	0.0	645
		Ylg.	45.4	27.2	2.0	5.4	16.0	2.1	1.5+	0.4	1402
											2047
		Chi-sq.	1.6	0.1	2.3	0.3	5.1	1.0	9.7	2.3	22.3***
1969-1970	Breed.	Adult	45.2-	21.4	3.3	11.8	13.4+	1.5	1.2	2.2	1503
		Ylg.	51.4+	19.8	3.6	9.7	10.2-	2.0	0.6	2.6	1096
											2599
		Chi-sq.	5.0	0.7	0.3	2.7	5.4	1.1	2.1	0.5	17.9*

Table 7. Continued.

Years	Period	Age	Behavior								
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N
	Post.	Adult	53.2	16.7-	0.7	11.4-	9.9	4.8+	1.8	1.4	1754
		Ylg.	49.5	19.8+	0.9	14.0+	9.3	3.4	2.1	1.2	2728
											4480
		Chi-sq.	2.2	6.1	0.3	6.2	3.0	5.1	0.5	0.5	23.8***
	Fall.	Adult	52.8	18.4-	2.5	10.1	13.4+	2.3	0.0-	0.6	843
		Ylg.	50.4	23.5+	2.6	10.4	10.1-	2.0	0.7+	0.4	2098
											2941
		Chi-sq.	0.7	7.0	0.0	0.1	5.9	2.0	5.6	0.6	20.1**

* = significant at .05.
** = significant at .01,
*** = significant at .005.

Table 8. Comparisons of the relative frequencies of eight behaviors of adult and yearling female Uinta ground squirrels during the gestation, lactation and postbreeding periods of high population density years (1965 and 1966) and of low population density years (1969 and 1970). Behavior frequency displayed as percentage.

Years	Period	Age	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
1965-1966	Gest.	Adult	55.8	12.2	2.5	7.4+	12.0	5.4	4.1	0.6	4746
		Ylg.	58.2	12.4	2.7	6.3-	11.3	4.8	3.9	0.4	4748
											9494
		Chi-sq.	2.4	0.2	0.3	4.7	1.1	1.2	0.3	2.6	12.8
	Lact.	Adult	59.7	16.2	1.6	9.6	6.4-	1.7	3.5	1.2	4407
		Ylg.	57.0	17.4	2.1	8.6	7.9+	1.7	4.1	1.2	4305
											8712
		Chi-sq.	2.8	1.8	3.3	2.6	6.8	0.0	1.9	0.0	19.2**
	Post.	Adult	51.1	16.2-	1.9	11.2	10.9	3.6+	3.2+	1.9+	863
		Ylg.	53.9	21.6+	1.4	9.0	10.4	1.9-	1.6-	0.2-	1336
											2199
		Chi-sq.	0.8	7.9	0.6	2.7	0.1	6.1	6.6	16.1	40.9***
1969-1970	Gest.	Adult	57.8+	11.3	1.6	8.2-	13.3	4.7	2.5	0.7	2444
		Ylg.	53.1-	12.5	1.6	11.9+	13.3	4.5	1.8	1.3	1830
											4274
		Chi-sq.	4.1	1.4	0.0	14.1	0.0	0.1	2.3	3.5	25.5***

Table 8. Continued.

Years	Period	Age	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
	Lact.	Adult	56.8+	16.5	0.8	13.5	6.7	2.2-	1.9-	1.6	3496
		Ylg.	51.0-	18.7	1.2	14.3	6.9	3.4+	3.0+	1.6	2305
											5801
		Chi-sq.	8.5	3.7	2.5	0.6	0.1	6.9	7.3	0.0	29.5***
	Post.	Adult	54.4	18.1	1.7	9.2-	13.5+	2.7	0.1	0.4	1045
		Ylg.	58.0	16.0	1.4	12.8+	8.5-	2.6	0.3	0.5	1172
											2217
		Chi-sq.	1.3	1.5	0.5	6.5	12.5	0.0	0.8	0.2	23.3***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

difference in frequency of a specific behavior observed. During the breeding periods of the composite high and low density years, yearling males fed more frequently than did adults.

The most consistent pattern of frequency of specific behaviors that was observed was no difference in frequency between adults and yearlings. Among both males and females there were no difference in frequencies of encounters between age classes during any period.

Among males the common patterns of frequency of specific behaviors were no differences in frequency of feeding, upright, grooming and calling behaviors during the fall periods of the seasons and no differences in frequency of nest gathering during the breeding and postbreeding periods of the season.

Among females there were no consistent patterns of differences in frequency of specific behaviors. The common patterns of frequency of behavior were no differences in frequency of feeding during postweaning, of moving, motionless, grooming and nest gathering during gestation and of calling during lactation.

After examining the consistent patterns of frequencies of specific behaviors during similar periods it appears that age alone is not a primary factor influencing behavior frequency among ground squirrels. Rather, circumstantial factors are more important. One likely factor is population density. For example, Slade and Balph (1974) reported that after the population was artificially reduced, yearling males exhibited more adult-like sexual behavior than during the high density years.

Comparisons of the behavior of squirrels during years of high and low population density. The influence of population density upon

behavior frequency was assessed by summing the data of squirrels of like sex and age classes and of like sex during years of similar population density, then comparing the behavior frequencies of like groups during similar periods of the season of the high and low density years (Tables 9 and 10). Additional inferences of population density on behavior were drawn from Tables 6 through 8. The manner in which like sex and age classes and like sex groups apportioned their time in the eight behaviors during similar periods of the seasons of high and low density years were significantly different ($P<.005$, 7 df) in all comparisons (Tables 9 and 10). Thus the probability of an association between population density and frequency of specific behaviors is high,

Patterns of frequencies of specific behaviors between animals of like sex and age class and like sex of high and low density years were variable (Tables 9 and 10).

Among males, the most common pattern of feeding frequency between adult males and between yearling males of high and low density years (Table 8) was no difference in behavior frequencies (four of six comparisons). However, when all males were compared as a group, the primary pattern was a higher frequency of feeding among males of the low density years than among males of the high density years (two of three comparisons).

The primary pattern of moving between adult males, yearling males and all males as a group was a higher frequency during years of high density than during years of low density (three of three, two of three, and three of three comparisons, respectively). The common pattern of encounters for males was no difference in frequency

Table 9. Comparisons of the relative frequencies of eight behaviors of male Uinta ground squirrels during similar periods of the seasons during high and low population density years. Behavior frequency displayed as percentage.

Age	Period	Pop. Density	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
Ad.	Breed.	High	38.9-	35.2+	3.6	7.2-	9.0-	2.0	0.7	3.4	3346
		Low	45.2+	21.4-	3.3	11.8+	13.4+	1.5	1.2	2.2-	1503
											4849
		Chi-sq.	10.2	64.6	0.3	25.5	19.4	1.5	3.2	4.8	129.4***
	Post.	High	52.0	20.5+	1.3	7.8-	7.9-	4.5	5.6+	0.4-	1817
		Low	53.2	16.7-	0.7	11.4+	9.9+	4.8	1.8-	1.4+	1754
											3571
		Chi-sq.	0.3	6.8	2.9	12.4	4.0	0.1	34.7	9.4	70.6***
	Fall	High	49.5	27.9+	3.1	4.8-	11.9	2.8	0.0	0.0-	645
		Low	52.8	18.4-	2.5	10.1+	13.4	2.3	0.0	0.6+	843
											1488
		Chi-sq.	0.8	14.7	0.5	13.1	0.6	0.4	0.0	3.8	33.8***
Ylg.	Breed.	High	48.6	26.3+	3.6	5.2-	10.4	3.3	0.8	1.9	1980
		Low	51.4	19.8-	3.6	9.7+	10.2	2.0-	0.6	2.6	1096
											3076
		Chi-sq.	1.1	12.5	0.0	21.3	0.0	4.1	0.1	2.0	41.1***
	Post.	High	46.6	21.7	1.9+	6.3-	11.9+	5.2+	5.3+	1.1	2650
		Low	49.5	19.8	0.9-	14.0+	9.3-	3.4-	2.1-	1.2	2728
											5378
		Chi-sq.	2.3	2.4	10.5	76.6	8.2	10.2	39.2	0.1	149.4***
	Fall	High	45.4-	27.2+	2.0	5.4-	16.0+	2.1	1.5+	0.4	1402
		Low	50.4+	23.5-	2.6	10.4+	10.1-	2.0	0.7-	0.4	2098
											3500
		Chi-sq.	4.5	4.8	1.2	24.7	23.8	0.0	5.8	0.0	64.8***
All.	Breed	High	42.3-	31.7+	3.6	6.4-	9.5-	2.5	1.3	2.8	5357
		Low	47.8+	20.7-	3.4	10.9+	12.1+	1.7-	1.0	2.4	2599
											7956
		Chi-sq.	12.2	75.7	0.1	45.0	11.4	4.5	1.4	1.1	151.5***
	Post.	High	48.8	21.2+	1.7+	6.9-	10.3	4.9+	5.4+	0.8-	4467
		Low	50.9	18.6-	0.8-	13.0+	9.6	3.9-	1.9-	1.3+	4482
											8949
		Chi-sq.	2.0	7.7	13.0	82.2	1.1	4.8	73.5	4.2	188.7***
	Fall	High	46.7-	27.5+	2.3	5.2-	14.8+	2.3	1.0+	0.2	2047
		Low	51.1+	22.0-	2.6	10.3+	11.1-	2.1	0.5-	0.4	2941
											4988
		Chi-sq.	4.9	14.8	0.2	37.8	13.2	0.3	5.2	1.3	77.7***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

Table 10. Comparisons of the relative frequencies of eight behaviors of female Uinta ground squirrels during similar periods of the seasons of high and low population density years. Behavior frequency displayed as percentage.

Age	Period	Pop. Density	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest.	Call.	N
Ad.	Gest.	High	55.8	12.2	2.5+	7.4	12.0	5.4	4.1+	0.6	4746
		Low	57.8	11.3	1.6-	8.2	13.3	4.7	2.5-	0.7	2444
											7190
		Chi-sq.	1.1	1.1	6.6	1.3	1.9	1.3	11.5	0.2	25.1***
	Lact.	High	59.7	16.2	1.6+	9.6-	6.4	1.7	3.5+	1.2	4407
		Low	56.8	16.4	1.2-	11.3+	6.6	1.9	2.8-	1.4	3496
											7903
		Chi-sq.	2.8	0.1	9.7	25.2	0.3	3.1	18.1	1.7	61.1***
	Post.	High	51.1	16.2	1.9	11.2	10.9	3.6	3.2+	1.9+	863
		Low	54.4	18.1	1.7	9.2	13.5	2.7	0.1-	0.4-	1043
											1908
		Chi-sq.	0.9	1.0	0.0	2.0	2.6	1.3	30.8	9.8	48.4***
Ylg.	Gest.	High	58.2+	12.4	2.7+	6.3-	11.3	4.8	3.9+	0.4-	4748
		Low	53.1-	12.5	1.6-	11.9+	13.3+	4.5	1.8-	1.3+	1830
											6578
		Chi-sq.	6.0	0.0	6.6	52.6	4.4	0.3	16.9	16.3	103.0***
	Lact.	High	57.0+	17.4	2.1+	8.6-	7.9	1.7-	4.1+	1.2	4305
		Low	51.0-	18.7	1.2-	14.3+	6.9	3.4+	3.0-	1.6	2305
											6610
		Chi-sq.	9.7	1.3	6.7	45.8	2.1	18.1	4.7	1.4	89.8***
	Post.	High	53.9	21.6+	1.4	9.0-	10.4	1.9	1.6+	0.2	1336
		Low	58.0	16.0-	1.4	12.8+	8.5	2.6	0.3-	0.5	1172
											2508
		Chi-sq.	1.9	10.6	0.0	8.4	2.3	1.3	11.3	1.4	37.3***
All.	Gest.	High	56.9	12.3	2.6+	6.9-	11.7-	5.1	4.0+	0.6-	9501
		Low	55.8	11.8	1.6-	9.8+	13.3+	4.6	2.2-	0.9+	4274
											13775
		Chi-sq.	0.7	0.6	13.4	32.6	6.3	1.3	27.0	5.8	87.7***
	Lact.	High	58.4+	16.8	1.8+	9.1-	7.2	1.7-	3.8+	1.2	8712
		Low	54.5-	17.4	1.0-	13.8+	6.8	2.7+	2.3-	1.6	5801
											14513
		Chi-sq.	9.2	0.6	18.1	69.0	0.7	16.3	22.9	3.3	140.0***
	Post.	High	52.8	19.5+	1.6	9.9	10.6	2.5	2.2+	0.9	2199
		Low	56.3	17.0-	1.5	11.1	10.9	2.6	0.2-	0.5	2217
											4416
		Chi-sq.	2.5	3.9	0.0	1.6	0.1	0.0	38.6	2.9	49.6***

* = significant at .05.
** = significant at .01.
*** = significant at .005.

between like groups of high and low density years (three of three, two of three, and two of three comparisons, respectively). In all comparisons, upright behavior was exhibited at a higher frequency by animals of the low density years than by animals of the high density years.

Patterns of frequency of remaining motionless were specific to each group of males considered. Between adult males motionless frequency was higher among adults of low density years than among adults of the high density years (two of three comparisons). Between yearling males there was a higher frequency among yearlings of the high density years than during the low density years (three of three comparisons). There was no consistent pattern of motionless frequency between years when all males of similar density years were compared.

Patterns of grooming frequency were age related. Between adult males of high and low densities, the basic pattern was no difference in grooming frequency (three of three comparisons). Between yearling males and all males as a group, animals of the low density years tended to groom less frequently than did animals of the high density years (two of three comparisons, respectively).

No consistent pattern was noted for the frequencies of nest gathering between adult males of high and low density years. Between yearlings and all males as a group, animals of the low density years gathered nest material less frequently than did like animals of the high density years (two of three comparisons, respectively). The common patterns of calling frequency between yearlings and all males was no difference in frequency between animals of high and low density

years (two of three comparisons, respectively). However, adult males of the low density years tended to call more frequently than did adult males of the high density years (two of three comparisons).

Differences also were observed in the behavior frequencies of adult and yearling males during similar periods of similar population density years (Table 7). Adults of low density years tended to be motionless more frequently than did yearlings (two of three comparisons). This pattern was reversed during the high density years (two of three comparisons).

As with males, the patterns of frequencies of specific behaviors between groups of females were also variable (Table 10).

Moving, motionless and grooming behaviors of adults, yearlings and all females as a group showed no differences in frequency between animals of high and low density years (three of three, two of three, and two of three comparisons, respectively). The primary pattern of encounters and nest gathering for these groups was a higher frequency among animals of the high density years than among animals of the low density years (two of three comparisons, respectively, for encounters and three of three comparisons, respectively, for nest gathering).

Patterns of feeding, upright and calling frequencies were variable between groups of females. For adult females, the common pattern was no difference in frequencies between high and low density years (three of three comparisons for feeding and two of three comparisons, respectively, for upright and calling). For yearling females, feeding frequency was lower among squirrels of

low density years than for squirrels of high density years (two of three comparisons). Higher frequencies of upright behavior were observed for yearlings of low density years than for yearlings of high density years (three of three comparisons). The pattern for calling was no difference in frequency between yearlings of high and low density years (three of three comparisons). Among all females, there were no differences in frequencies of feeding between animals of high and low density (three of three comparisons). The common pattern for upright and calling between all females was a higher frequency by animals of the low density years than by animals of the high density years (two of three comparisons, respectively).

Differences also were observed in the behavior frequencies of adult and yearling females during like periods of similar population density years (Table 8). During low density years yearlings tended to feed less frequently and assumed the upright posture more frequently than did adults (two of three comparisons, respectively). During the years of high density there tended to be no differences in the frequencies of these behaviors between adults and yearlings (three of three comparisons and two of three comparisons, respectively).

An association between population density and the manner in which males and females apportioned their behavior during comparable periods was also observed (Table 6). During high density years females tended to have higher frequencies of upright behavior than did males (two of three comparisons). During years of low population density the pattern of being upright was no difference in frequency between males and females (three of three comparisons). The primary patterns of motionless frequency between males and females were a higher

The observed associations between population density and behavior frequency were related to sex or sex and age classes of the animals compared. In general, there were fewer differences in frequency of behavior between males of high and low density years than between females. Also there were fewer differences in frequency of behavior between yearlings of low and high density years than between adults. I suspect that these differences are related to the dominance relationships between individuals of different sex and age classes and the differential orientation of aggression between sex groups. In general, females were dominant to males and adults were dominant to yearlings (Burns 1968, Paul 1977). Paul (1977) also reports that while females were aggressive to all conspecifics, males tended to be aggressive only to other males.

When data for high and low population density years were compared no differences in frequencies of moving, motionless or grooming behaviors among females as a group or within one age class were found. However, the frequencies of encounters and nest gathering were higher during the high density years than during the low density years. Given that females are aggressive to all conspecifics and that the conditions that elicit aggression are more likely to be encountered during high density years, the higher rates of aggression during high density years should be expected. The higher frequencies of nest gathering during high density years is difficult to justify as a density related behavior. However, nest gathering was often associated with calling by the animal. Often when returning to the burrow with nest material an animal would stop at the burrow,

come upright and churr. The function of the churr is to threaten other animals and inhibit them from moving closer (Balph and Balph 1966). During years of high density, with larger numbers of conspecifics about or in the individual's home range, high frequencies of nest gathering, if associated with an aggressive animal, may reduce intrusion by conspecifics into an animal's core area. An alternative hypothesis would be that the higher frequencies of nest gathering during high density years is a displacement response to the high frequency of conflict situations associated with high encounter frequency. Additional work needs to be conducted to assess the functional aspects of nest gathering in high and low population density years.

In addition to the patterns of behavior frequencies shared with adult females, the behavior frequencies of feeding and upright by yearlings also differed during high and low density years. During years of low density, yearlings fed less frequently than did yearlings of high density years and yearlings as a group fed less frequently than did adults as a group. Concomitantly, yearlings of low density years were upright more than yearlings of high density years and yearlings as a group were upright more than adults as a group. These differences are likely associated with yearlings being subordinate to adults and the differential use of the lawn and nonlawn areas by yearlings during high and low density years. During the high density years, 16 percent of the yearlings resided in the lawn. After the population reduction, 42 percent of the yearlings lived on the lawn. The proportion of adult females

(approximately 32 percent) living on the lawn was not different during high and low density years (Slade and Balph 1974). Cooper and Levine (1973) concluded from a laboratory study that Peromyscus spp. are socially inhibited from feeding and drinking in pairs. Should this observation be applicable to Uinta ground squirrels, the presence of a conspecific in the immediate area may reduce feeding frequencies. Given that a larger percentage of yearlings lived in the high density lawn area during low density years and that adults tend to be dominant, the low frequency of feeding and the high frequency of upright may result from the greater association by yearlings with the more aggressive adults.

Although there were no differences in calling frequency between adults or yearlings of high and low density years, the primary pattern of calling frequency when all age groups were pooled was a higher frequency of calling by females of the high density years. Given that high density conditions are more likely to be conducive of those conditions that elicit aggression, the high frequency of calling during high density years is not surprising.

Consistent patterns of frequency were observed for moving and upright behavior between adult males of high and low density years. Between all groups, moving was most frequent during high density years and upright behavior was most frequent during low density years. Given that males were similarly dispersed in the study area during high and low density years (Slade and Balph 1974) and that the principal role of the male is to breed and repulse competing males, the high frequency of moving during high density years is

probably the result of larger numbers of social interactions during those years. If upright behavior also functions to help the male assess the proximity of females, then a high frequency of upright behavior in an environment with dispersed conspecifics would be advantageous.

I cannot explain the high frequency of motionless behavior by adult males during low density years. However, the higher frequency of motionless behavior of males relative to females (Table 6) may be related to males intruding into areas of high female density and being motionless more frequently as the result of proximity of the more aggressive females.

Between yearling males of high and low density years, motionless, grooming and nest gathering were more frequent during high density years than during low density years. During high density years, yearling males were subordinate to all conspecifics except juveniles. I suspect that the high frequencies of these behaviors are the result of the low social rank of yearling males and the high frequency of social interactions during the high density years.

When all males were considered as a group, the frequency of feeding during low density years was higher than during high density years and nest gathering frequency was lower during low density years than during high density years. These patterns are consistent with the effects of density on feeding and nest gathering proposed earlier.

In conclusion, there are real associations between behavior frequency and population density among Uinta ground squirrels. It is likely that the relationship is mediated by the sex of the

animal, the effective densities at various sites within the study area and the dominance relationship of sex and age groups within the population. Differential response patterns between sexes would be consistent with the promiscuous breeding system of the Uinta ground squirrel. Each sex plays different roles; hence, each should show responses consistent with those roles. For example, females should show high frequencies of those behaviors which insure them of an area in which to rear young, and males should show high frequencies of those behaviors which increase the opportunity to breed.

Behavior in relation to habitat. At the study area, ground squirrels occupied two basic habitat types, the lawn about the station buildings and the nonlawn area dominated by sagebrush (Artemisia tridentata) with native grasses (Walker 1968). This situation allowed an opportunity to examine the possible relationship between habitat and behavior among groups of animals. Comparisons were made between the behavior of animals when in the lawn and when in the sage-grass habitat. Comparisons were limited to those sex and age groups having 100 or more observations in both habitats per seasonal period. Five groups of males and nine groups of females were selected for comparisons (Tables 11 and 12).

Males in the lawn and nonlawn habitats apportioned their time spent in the eight behaviors differently ($P<.10$) in 11 of 13 comparisons. Concomitantly, females apportioned their time spent in the eight behaviors differently in the lawn and in the sage-grass habitats ($P<.10$) in 17 of 20 comparisons. Thus, it would appear

Table 11. Comparisons of the relative frequencies of eight behaviors within groups of male Uinta ground squirrels while occupying lawn and nonlawn habitats. Behavior frequency displayed as percentage.

Year/ Group	Period	Habitat	Behavior: Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	N.
	Breed.	Lawn	46.7+	28.4-	5.8+	5.6	7.2	0.6	0.4	5.4	503
1965		Nonlawn	36.9-	45.1+	1.5-	4.4	6.4	1.4	0.2	4.1	590
Ad. 0.9											1093
		Chi-sq.	6.3	20.1	14.0	0.7	0.2	1.6	0.5	1.0	44.4***
	Post.	Lawn	58.2	12.5-	3.2+	6.4	9.8+	3.9	5.4	0.5	407
		Nonlawn	57.8	22.5+	0.0-	7.9	2.8-	3.1	4.8	0.9	351
											758
		Chi-sq.	0.0	10.9	11.2	0.7	13.9	0.3	0.1	0.4	37.6***
	Fall	Lawn	52.0	26.8	3.1	2.4	12.6	4.7	0.0	0.0	127
		Nonlawn	55.4	32.0	3.2	0.5	7.7	1.4	0.0	0.0	222
											349
		Chi-sq.	0.2	0.7	0.0	2.6	2.1	1.3	0.0	0.0	6.9
1966	Breed.	Lawn	41.6	29.0-	4.2	7.4	11.8	2.3	0.3	3.3	692
Ad. 0.9		Nonlawn	38.5	37.1+	2.9	9.3	8.8	1.4	0.1	1.8	782
											1474
		Chi-sq.	0.9	7.1	1.6	1.7	3.3	1.6	0.5	3.4	20.2**
	Post.	Lawn	44.8	22.8	0.0-	0.2-	12.8	7.2+	9.3	0.7	290
		Nonlawn	44.2	24.9	1.9+	11.5+	8.6	3.3-	5.6	0.0	269
											559
		Chi-sq.	0.0	0.3	5.4	17.0	2.3	3.9	2.6	1.9	33.4***
1966	Breed.	Lawn	40.9+	29.3-	4.4	9.6+	7.7	3.9	0.7-	3.5	457
Ad. 10-19		Nonlawn	27.4-	42.9+	2.5	5.6-	11.9	2.8	4.2+	2.5	354
											811
		Chi-sq.	10.4	10.5	1.9	4.0	3.7	0.7	11.5	0.6	43.3***
	Post.	Lawn	52.4+	17.4	1.5-	8.7-	11.0	5.1+	3.6	0.3-	391
		Nonlawn	33.9-	11.7	5.3+	18.7+	9.4	0.0-	3.5	17.5+	171
											562
		Chi-sq.	8.7	2.5	6.2	10.2	0.3	8.7	0.0	64.5	101.1***
1966	Breed.	Lawn	53.2	24.5	3.4	4.3	12.4	0.0-	0.9	1.3	233
Ylg. 20-29		Nonlawn	53.4	19.8	3.1	4.2	12.2	5.0+	0.0	2.3	262
											495
		Chi-sq.	0.0	1.2	0.1	0.0	0.0	11.6	2.2	0.7	15.7*
	Post.	Lawn	42.2	23.9	1.1	9.5	12.3	5.6	4.5+	1.5	268
		Nonlawn	44.6	27.8	0.5	9.6	8.9	5.8	1.5-	1.3	395
											663
		Chi-sq.	0.2	1.0	0.8	0.1	1.9	0.0	5.1	0.1	9.1
	Fall.	Lawn	40.5	30.3	3.4+	5.0-	18.3+	2.0	0.2-	0.2	442
		Nonlawn	44.4	27.1	0.3-	10.5+	11.7-	3.4	2.6+	0.0	266
											708
		Chi-sq.	0.6	0.6	6.7	7.2	4.7	1.2	8.5	0.6	30.1***
1970	Breed.	Lawn	50.4+	22.5	1.3-	8.2-	15.4	0.7	0.7	0.7	837
Ad. 0-9		Nonlawn	36.2-	22.1	9.1+	16.6+	11.4	2.2+	0.0	2.2+	307
											1144
		Chi-sq.	9.8	0.0	40.2	15.0	2.5	4.8	2.2	4.8	79.3***

Table 11. Continued.

Year/ Group	Period	Habitat	Behavior							N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
	Post.	Lawn	53.6	17.9	0.6	11.5	12.2	3.1	0.5-	0.6-	817
		Nonlawn	51.5	19.5	1.3	11.0	8.0-	4.3	2.4+	2.0+	538
											1355
		Chi-sq.	0.3	0.5	1.7	0.1	5.5	1.4	9.6	5.6	24.7***
	Fall	Lawn	44.0	23.8	2.1	8.8	18.8+	2.3	0.0	0.2	432
		Nonlawn	49.0	18.3	3.9	13.7	9.8-	3.3	0.0	2.0+	153
											583
		Chi-sq.	0.6	1.5	1.5	2.7	5.5	0.4	0.0	4.9	17.2**

* = significant at .05.
** = significant at .01.
*** = significant at .005.

Table 12. Comparisons of the relative frequencies of eight behaviors within groups of female Uinta ground squirrels while occupying lawn and nonlawn habitats. Behavior frequency displayed as percentage.

Year/ Group	Period	Habitat	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
1965 Ad. 0-9	Gest.	Lawn	53.1	6.3-	5.9+	7.2	11.8+	10.9+	3.6-	1.3	697
		Nonlawn	53.8	17.6+	1.6-	7.8	7.6-	3.3-	7.6+	0.7	448
											1145
		Chi-sq.	0.0	32.5	12.1	0.1	4.7	19.6	8.5	1.0	78.6***
	Lact.	Lawn	69.2+	11.0-	3.6+	6.8-	4.0	2.2	2.5	0.8	973
		Nonlawn	57.8-	20.7+	0.4-	10.1+	4.9	1.2	4.0	0.9	773
											1746
		Chi-sq.	8.6	26.5	20.4	5.7	0.8	2.5	3.3	0.0	67.8***
1965 Ad. 10-19	Gest.	Lawn	59.3	12.7	1.9	9.4	8.0	3.9	3.6	1.1	361
		Nonlawn	59.9	12.7	3.2	8.4	8.1	3.2	3.5	1.1	347
											708
		Chi-sq.	0.0	0.0	1.1	0.2	0.0	0.3	0.0	0.0	1.6
	Lact.	Lawn	77.6+	7.4-	0.9	5.6-	3.5	1.2	3.2	0.6	339
		Nonlawn	58.1-	13.7+	0.0	17.6+	5.7	2.2	0.9	1.8	227
											566
		Chi-sq.	7.4	5.4	2.0	18.8	1.5	0.9	3.3	1.8	41.1***
1965 Ylg. 0-9	Gest.	Lawn	64.2	6.5-	4.8+	7.3	9.0	5.2	2.7	0.4	821
		Nonlawn	62.3	17.4+	0.8-	3.8	8.1	5.1	1.7	0.8	236
											1057
		Chi-sq.	0.1	24.6	7.2	3.4	0.2	0.0	0.7	0.9	37.1***
	Lact.	Lawn	64.0	9.0-	4.1+	10.7-	7.7+	2.3	1.9-	0.4	1056
		Nonlawn	60.6	19.7+	0.0-	5.7-	1.1-	0.4-	11.5+	1.2	279
											1335
		Chi-sq.	0.4	22.6	11.4	5.6	15.3	4.3	52.0	2.0	113.5***
1965 Ylg. 10-19	Gest.	Lawn	61.7+	9.8-	3.6	6.0	8.8-	6.3+	3.5	0.3	635
		Nonlawn	46.0-	22.7+	3.1	7.5	13.7+	3.1-	3.6	0.3	387
											1022
		Chi-sq.	10.7	27.6	0.2	0.8	5.4	4.8	0.0	0.0	49.5***
	Lact.	Lawn	59.1	16.3-	3.4+	7.7	5.8	1.6	5.2	0.8	729
		Nonlawn	55.2	26.0+	0.4-	10.4	2.8	0.4	3.2	1.6	250
											979
		Chi-sq.	0.5	9.3	6.4	1.6	3.3	2.2	1.6	1.1	26.0***
1966 Ad. 0-9	Gest.	Lawn	53.2	12.1	3.2	0.6	17.4	5.3	2.1	0.4	528
		Nonlawn	55.7	16.1	1.6	6.5	13.8	3.0	3.0	0.2	429
											957
		Chi-sq.	0.3	2.7	2.4	0.0	2.0	2.9	0.8	0.2	11.2
	Lact.	Lawn	61.2	13.3-	2.3	6.1	8.2	1.7	4.7	2.7+	709
		Nonlawn	57.8	20.6+	0.8	9.3	8.9	1.3	1.3-	0.0-	237
											946
		Chi-sq.	0.3	6.5	1.9	2.7	0.1	0.2	5.4	6.4	23.4***
1966 Ad. 10-19	Gest.	Lawn	60.9+	10.4-	1.9	6.5	12.0	4.9	3.2	0.2	925
		Nonlawn	52.4-	15.5+	1.3	8.3	13.5	5.2	3.4	0.4	1007
											1932
		Chi-sq.	6.1	9.7	1.3	2.2	0.9	0.1	0.0	0.5	20.7***

Figure 12. Continued.

Year/ Group	Period	Habitat	Behavior								N
			Feed.	Mov.	Enc.	Upr.	Mot.	Groom.	Nest G.	Call.	
	Lact.	Lawn	58.4+	17.1-	1.1	10.4-	8.4	1.6	1.9-	1.1	730
		Nonlawn	37.3-	25.7+	0.9	15.8+	9.6	2.2	6.5+	2.2	697
											1417
		Chi-sq.	32.9	12.3	0.2	7.9	0.6	0.5	17.8	2.5	74.6***
1966	Gest.	Lawn	58.2	9.3-	2.4+	5.4	11.4+	4.2	8.6	0.5	849
Ylg. 10-19		Nonlawn	57.5	18.8+	0.5-	3.8	7.5-	5.5	6.3	0.1	784
											1633
		Chi-sq.	0.0	26.3	9.4	2.2	6.5	1.3	3.0	1.6	50.3***
	Lact.	Lawn	55.7	17.2-	1.7	11.4+	6.6-	1.7	4.1	1.7	711
		Nonlawn	50.3	26.2+	0.7	6.7-	10.0+	1.6	2.1	2.3	608
											1319
		Chi-sq.	1.8	12.4	2.9	7.7	4.7	0.0	3.1	0.6	33.9***
1970	Gest.	Lawn	64.3+	10.9	0.5-	9.4	8.0-	4.3	2.4	0.3	588
Ad. 10-19		Nonlawn	51.1-	10.5	3.3+	7.9	18.5+	4.2	3.9	0.6	696
											1284
		Chi-sq.	9.6	0.0	12.3	0.8	25.8	0.0	2.2	0.4	51.2***
	Lact.	Lawn	61.2+	12.3-	0.5	14.6+	7.3	1.8	1.7	0.5-	949
		Nonlawn	52.0-	26.6+	0.7	7.3-	8.2	1.7	1.2	2.4+	723
											1672
		Chi-sq.	6.1	44.9	0.2	19.1	0.4	0.0	0.5	10.4	81.7***
	Post.	Lawn	62.5+	15.1	0.6	10.6	9.3-	1.0	0.0	1.0	312
		Nonlawn	39.1-	16.4	2.7	10.0	28.2+	3.6	0.0	0.0	110
											422
		Chi-sq.	7.9	0.1	3.0	0.0	20.4	3.5	0.0	1.1	36.0***
1970	Gest.	Lawn	58.5+	10.1	1.7	9.4	14.8	4.5	0.2-	0.8	533
Ylg. 20-29		Nonlawn	47.9-	12.0	2.6	7.2	19.8	5.4	3.7+	1.4	349
											882
		Chi-sq.	4.4	0.7	0.8	1.2	3.1	0.4	16.6	0.1	28.2***
	Lact.	Lawn	56.2	16.0-	0.7	10.6+	7.0	5.7+	2.1	1.5	667
		Nonlawn	54.3	25.5+	1.8	4.7-	7.1	2.1-	2.4	2.7	339
											1006
		Chi-sq.	0.2	10.2	2.1	9.1	0.0	6.6	0.1	1.6	29.9***
	Post.	Lawn	59.1	14.3	1.4	10.6	10.6	3.6	0.0	0.3	357
		Nonlawn	50.0	21.3	3.2	12.8	10.6	1.1	0.0	1.1	94
											451
		Chi-sq.	1.1	2.3	1.3	0.3	0.0	1.6	0.0	1.0	7.7

* = significant at .05.
** = significant at .01.
*** = significant at .005.

that the probability of a correlation between habitat and frequency of a specific behavior would be high.

The primary pattern of frequencies of specific behaviors by males in lawn and sage-grass habitats was no difference in behavior frequencies. No differences in frequency were found in 9 of 13 comparisons respectively of feeding, moving, motionless, nest gathering, grooming and calling behaviors, in 8 of 13 comparisons of upright, and in 7 of 13 comparisons of encounters. No other consistent patterns of behavior frequencies were observed when all comparisons were considered.

When comparing for differences in behavior during similar periods of the season, consistent differences were observed in the frequencies of feeding and moving in the two habitats by males during the breeding period. Feeding frequency was higher in the lawn habitat than in the sage-grass habitat, and moving was more frequent in the sage-grass areas than in the lawn (three of five comparisons each). There were no other consistent differences in frequencies of specific behavior between males in the two habitats during other periods of the season.

With the exception of feeding and moving during the breeding period, there appears to be no association between behavior and habitat type among males. The higher feeding frequency by males in the lawn may be in response to the greater abundance of foods in this habitat. Conversely, the higher frequency of moving by breeding males in the sage-grass areas may be partially influenced by the greater dispersion of food items in the nonlawn. An additional contributing factor may be the greater dispersion,

relative to the lawn, of conspecifics (Slade and Balph 1974). Since breeding males must explore to find receptive females, greater dispersion of conspecifics may contribute to the higher frequency of moving by males in the sage-grass habitat.

Consistent differences were observed in the frequencies of feeding and moving by females in the two habitats. Two patterns were observed for frequencies of feeding. One pattern was no differences in frequencies (14 of 20 comparisons). The other pattern was a higher frequency of feeding by females in the lawn than by females in the sage-grass areas (9 of 20 comparisons).

The primary pattern of moving was a higher frequency among females in the sage-grass areas than by females in the lawn (12 of 20 comparisons). The primary pattern for the remaining behaviors was no differences in frequency of behavior between animals in the two habitats. No difference in frequencies were found in 13 of 20 comparisons or encounters, in 11 of 20 comparisons of upright behavior, in 14 of 20 comparisons of motionless behaviors, in 16 of 20 comparisons of grooming, in 14 of 18 comparisons of nest gathering, and in 18 of 20 comparisons of calling. In addition, during high density years there tended to be a higher frequency of encounters by females in the lawn than in the nonlawn (6 of 14 comparisons).

The higher frequencies of feeding by females in the lawn may be a function of the greater availability and ease of access to foods. In addition, the use by sage-grass habitat residents of the lawn as feeding areas (Slade and Balph 1974) may be a factor

contributing to the high feeding frequencies by females in the lawn versus feeding in the sage-grass areas. Given the dispersed nature of foods in the sage-grass areas, increased frequency of moving to satisfy nutritional needs should be expected.

The high use levels of the lawn, the differential densities of females in the two habitats and the higher population densities of 1965 and 1966 (Slade and Balph 1974) are most likely contributing factors of the high frequency of encounters in the lawn during high density years. Slade and Balph note that there was a disproportional preference for the lawn among females as home range areas. In contrast, the home ranges of males were dispersed almost evenly throughout the study area. There were no differences in frequencies of encounters by males in the two habitats.

Although chi-square analysis would indicate a relationship between habitat and behavior of animals, only the frequencies of two behaviors, feeding and moving, were consistently associated with a given habitat. The lack of a more pronounced association can be due to a number of factors. One such factor would be the methodology of determining patterns of comparison frequencies. However, another factor is the resolution used in describing behavior. This analysis compared the frequencies of general categories of behavior. In various other studies that denote differences in behavior of a species between habitats, the differences are between components of a general category of behavior. For example, Barash (1973) noted differences in the frequency of components of aggressive behavior of two colonies of yellow-bellied marmots (Marmota flaviventris) in different habitats. Post and Greenlaw (1975)

observed differences in components of aggressive behavior of the seaside sparrow (Ammospiza maritima), but Post (1974) noted no differences in the general categories of amount of time spent in foraging, singing or resting of birds in two different habitat types. Kummer (1968) noted that Hamadryas baboons (Papio hamadryas) adapt various aspects of their feeding behavior to changing environmental conditions. Thus while the primary conclusion of the analysis of habitat and behavior of Uinta ground squirrels is that there appears to be little consistent association between behavior frequency and habitat, further study using more discrete descriptions of behavior may be able to show a more pronounced association.

General summary and conclusions

The primary purpose of this portion of research was to describe the time budgets of free-living ground squirrels and to determine the correlative relationships between behavior frequency and sex, age, population density and habitat.

The data presented were interpreted as evidence that Uinta ground squirrels organize their behavior diurnally and seasonally. In addition such factors as sex, age, population density and habitat all appear to influence the frequency of behavior. However, with the exception of differences in behavior frequency between sexes, much variation in differences of frequency of specific behaviors was observed.

Diurnal patterns of behavior were shaped by the cyclic pattern of feeding, the dominant behavior among ground squirrels. Among all animals, feeding tended to be most frequent during the first two

and last two hours of the day. As the frequency of feeding decreased during the midday, behavioral diversity increased. Thus, it was concluded that diurnal organization was determined largely by the cycle of nutrient requirements of the species.

Seasonal patterns of behavior were associated with the seasonal partitioning of reproductive events of each sex. Males were sexually active during the breeding and fall periods and those behaviors which were likely to contribute to increased opportunities of breeding were high. During the midperiod of the year behaviors that contributed to self-maintenance and fat deposition were frequent. There was an accent on maintenance-productivity behaviors among females. This emphasis is believed to be a response to the increased metabolic demands and maternal related behavior of lactating females. It was concluded that the seasonal organization of behavior among ground squirrels was fundamentally related to the physiological state of the animal. Among males, sexual behavior, hence high social interaction behaviors, coincides with the annual cycle of androgen synthesis. Among females, behavior is fundamentally related to the annual cycle of aggressiveness and the metabolic demands of gestation and lactation.

Additional differences were found in the comparisons of behavior between males and females. Females consistently fed more than males and males consistently moved more than females. Other differences in behavior frequently were restricted to specific periods of the season. For example, during the breeding/gestation period males encountered and called more than females and females gathered nest material more frequently than males. These differences appear to

be correlated with the different functional roles each sex plays in the population. The principal role of the male is to breed. Success in fulfilling this role is correlated with those behaviors which increase his opportunities to breed, i.e., moving, encountering and calling. During periods of sexual quiescence, self-maintenance behaviors which enhance chances of over-winter survival are adaptive. The principal role of the female is to reproduce. Her first problem is to locate an area providing sufficient resources for rearing of young. Relative to males, an accent on maintenance-productivity behaviors increases the chance of successful reproduction and over-winter survival among females.

Despite the differences in behavior between age groups of the same sex as determined by chi-square analysis, few consistent differences in behavior frequency throughout the season were noted. Those that were observed were restricted to specific periods of the year and are probably influenced by dominance relationships mediated by population density. The lack of consistent differences in behavior frequency throughout the season is likely influenced by the fact that all animals of a given sex group were experiencing similar physiological states during similar periods.

A number of differences were observed in behavior frequencies of like sex and age groups during years of high and low density. These differences were consistent with the aggressive responses of each sex group, the dominance relationships of sex and age groups and the functional objectives of each sex group. In general females showed more differences in frequencies of behaviors between

years of high and low density than did males. Concomitantly, yearlings showed some differences in frequencies of behaviors than did adults. Females have a greater tendency to respond aggressively to all other squirrels than do males. The higher frequencies of encounters, nest gathering and calling by females during high density years are assumed to be the result of more conspecifics being in or near the home range. The high frequency of moving during high density years and the high frequency of upright behavior during low density years by males was assumed to be responses to the differential numbers and dispersion of females during these years. The higher frequencies of grooming, motionless and nest gathering by yearling males during high density years were taken as evidence of displacement behavior by less dominant animals. During high density years, yearling males were subordinate to all but juveniles. The low frequency of feeding and high frequency of upright behavior among yearling females during the low density years was also taken as evidence of age related subordination since it was associated with a higher percentage of yearlings residing on the lawn with dominant adults than during the high density years. Thus it appears that behavior is affected by population density and that most of the differences can be related to the level of aggressive interactions expected of high and low density populations and age related dominance.

As was the case for behavioral differences between age groups, few consistent differences were noted when the behavior of like sex and age groups in lawn and sage-grass habitats were compared.

Consistent differences in frequency between habitats were found in only two behaviors. The frequency of feeding tended to be higher on the lawn than on the sage-grass areas and moving tended to be more frequent on the sage-grass areas than on the lawn. These differences were consistent with the dispersion of conspecifics and availability of foods between the two habitats.

In conclusion it does appear that the behavior of Uinta ground squirrels occurs in definite temporal relationships and their frequencies are affected by immediate environmental conditions. Given that the species occur in temperate environments characterized by daily and seasonal variation in biotic and abiotic conditions, consistent differences in frequencies of behavior should be expected if the animal is to optimally exploit available resources and time. The manner in which resources are exploited appears to be influenced by the functional roles of each sex and the social constraints associated with population density.

The Meteorological Environment and Its Influence On Daily Activity Patterns

Introduction

The ability of an individual to occupy a given area requires that the thermal exchange between itself and the environment be balanced. This exchange is continuous and its rate and direction of flow is determined by properties of both the animal and its microhabitat (King 1974, Moen 1973, Morhardt and Gates 1974). The physiochemical mechanisms of thermoregulation adequately regulate

the heat lost from the animal but are generally inappropriate for mediating the rate of heat gain (Bartholomew and Dawson 1968). As a result, the animal typically copes with heat stress by altering its activity pattern and/or by seeking microhabitats whose micrometeorological characteristics match its physical and chemical capacities of thermoregulation (Bartholomew and Dawson 1968, Bradley and Yousef 1972, Morhardt and Gates 1974 and others).

In recognition of the intrinsic tie between the animal and its meteorological environment, this aspect of the research was oriented to 1) describe the daily activity patterns of the Uinta ground squirrels, 2) describe their daily meteorological environments, 3) correlate the meteorological parameters with the energy exchange and activity of ground squirrels, and 4) evaluate squirrel use of alternate habitats in terms of their relative contributions to net energy exchange.

Methods

The data used in this section of the research were collected during the 1970 season. The homeothermic season of ground squirrels was divided into three periods each approximating the duration of a major reproductive event. These periods were the breeding/gestation period comprising the first 40 days of the season (April 4-May 13, 1970), the postbreeding/lactation period which made up the following 40 days of the season (May 14-June 21) and the fall/postweaning period which made up the last 40 days of the season (June 22-July 31).

Activity of ground squirrels, time spent above ground, was the basic variable used for correlation with meteorological (abiotic)

variables. Daily activity was described as the average hourly time ground squirrels were observed above ground during the first and last two hours of the day and of three three-hour intervals representing late morning, midday and early afternoon of a 13-hour day. Average hourly activity was calculated by dividing the total number of observations per period by the number expected if all target animals had been active during the period. Daily activity patterns were estimated from the data collected on the entire population of 1970.

The abiotic data measured were hourly measurements of ambient temperature, dew point, burrow temperature and wind speed collected concurrently with behavioral observations. These parameters were sampled in three vegetative types within the study site. These types were the lawn, an area of native grasses (field) and in an area with sage. Ambient and dew point temperatures were measured using thermistors and Lithiumcloride cells at 5 cm above the ground. Dew point was recorded at four different sampling points within each sample area. Ambient temperatures within the sampling areas were recorded at three different points above the ground and at 2 m from the entrance within a burrow.

Relative humidity was estimated from concurrent dew point and ambient temperature measurements. Wind speed was estimated with the Beaufort method and later correlated with wind speed measured by a micrometeorological cup anemometer at 10 cm above the ground. A correlation between the Beaufort scale and ground level wind speed was made in an open area and in an area with sagebrush overstory (Figure 1).

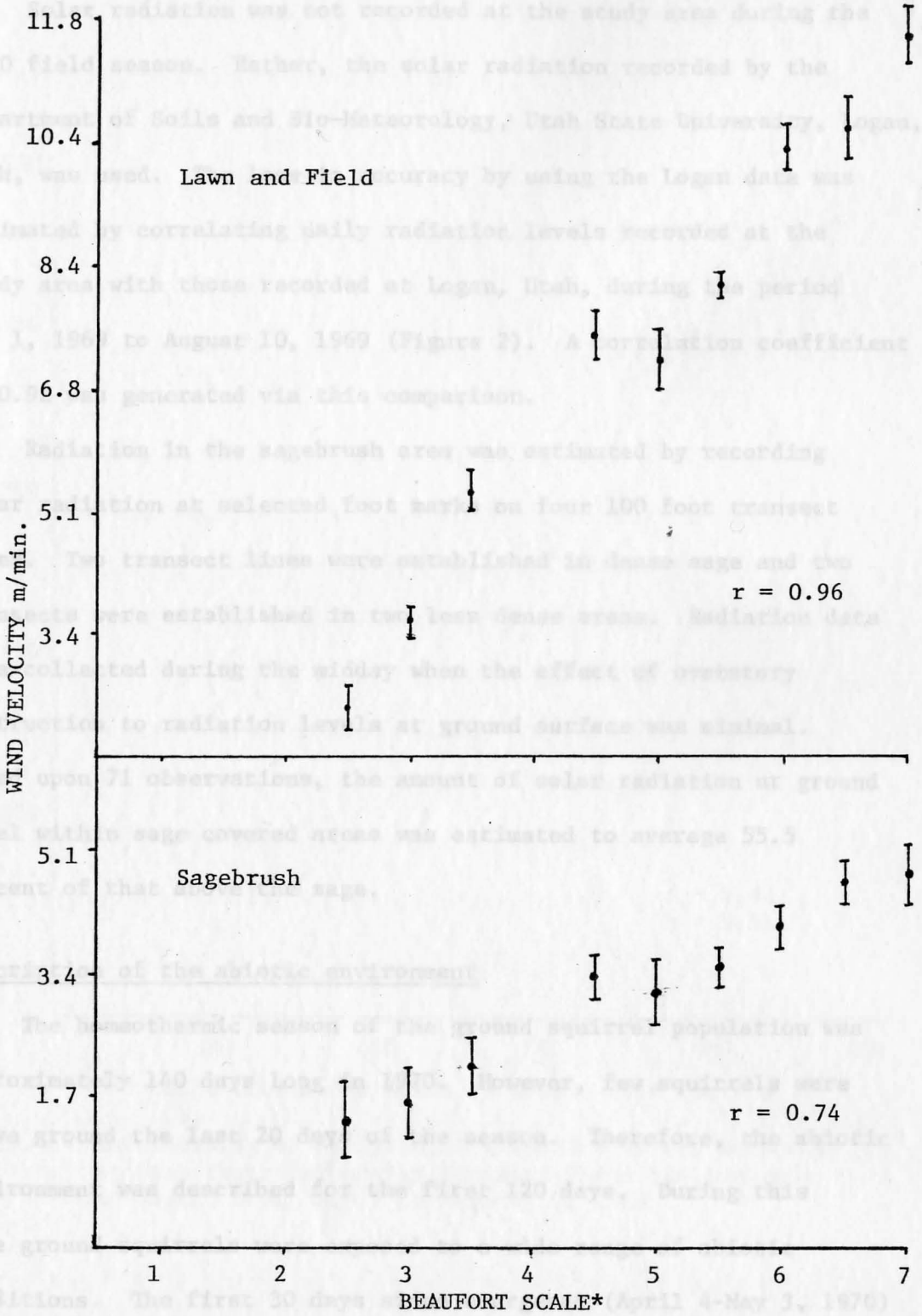

Figure 1. Relationship of ground wind velocity as measured by a micrometeorological cup anemometer and by the Beaufort method in lawn and sagebrush vegetation at Utah State University Forestry Field Station, 1970.

* List 1968.

Solar radiation was not recorded at the study area during the 1970 field season. Rather, the solar radiation recorded by the Department of Soils and Bio-Meteorology, Utah State University, Logan, Utah, was used. The loss in accuracy by using the Logan data was estimated by correlating daily radiation levels recorded at the study area with those recorded at Logan, Utah, during the period May 1, 1969 to August 10, 1969 (Figure 2). A correlation coefficient of 0.92 was generated via this comparison.

Radiation in the sagebrush area was estimated by recording solar radiation at selected foot marks on four 100 foot transect lines. Two transect lines were established in dense sage and two transects were established in two less dense areas. Radiation data were collected during the midday when the effect of overstory obstruction to radiation levels at ground surface was minimal. Based upon 71 observations, the amount of solar radiation at ground level within sage covered areas was estimated to average 55.5 percent of that above the sage.

Description of the abiotic environment

The homeothermic season of the ground squirrel population was approximately 140 days long in 1970. However, few squirrels were above ground the last 20 days of the season. Therefore, the abiotic environment was described for the first 120 days. During this time ground squirrels were exposed to a wide range of abiotic conditions. The first 30 days since emergence (April 4-May 3, 1970) of the first squirrel were characterized by unstable weather conditions, low ambient temperatures and high humidity levels

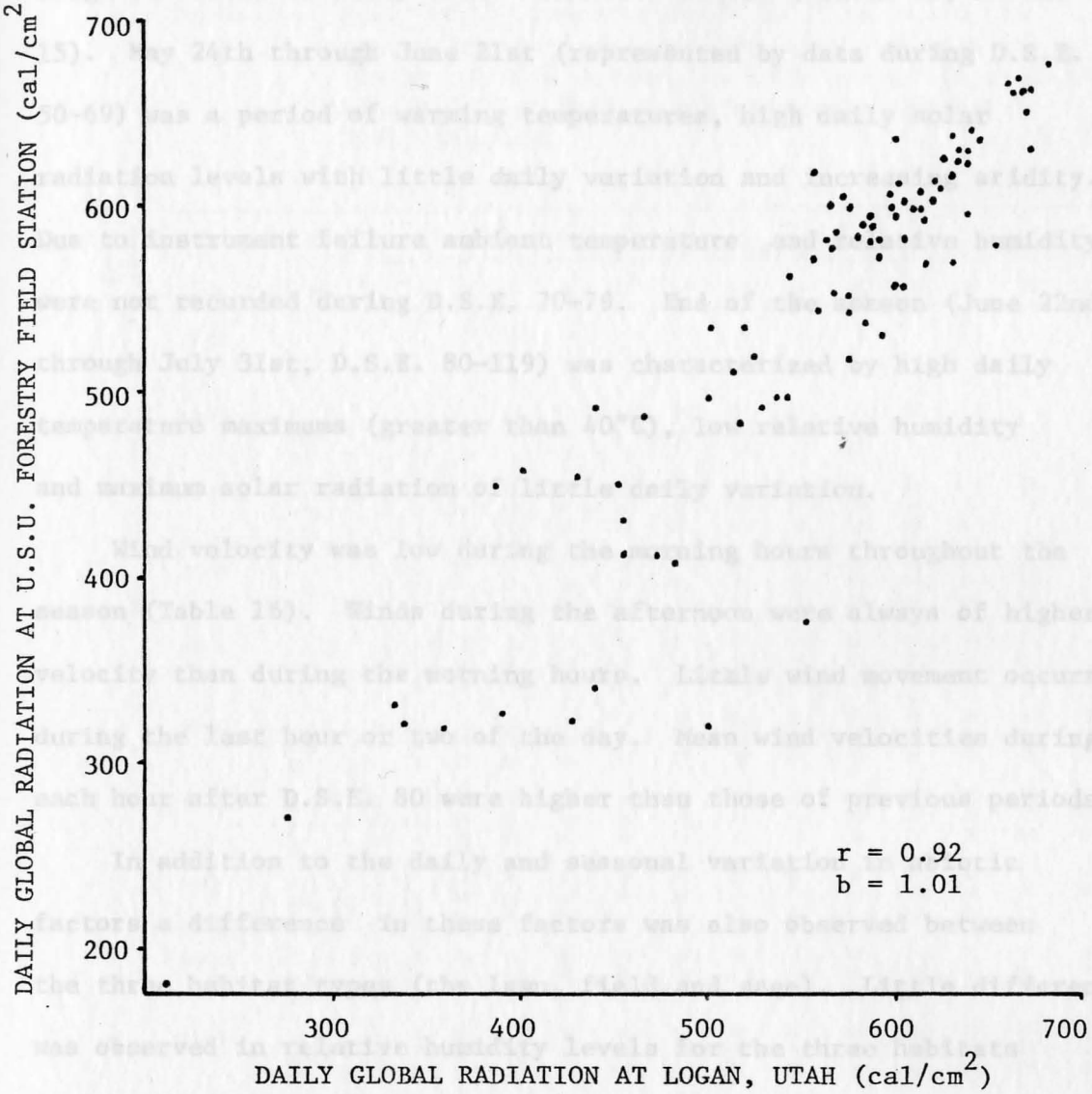

Figure 2. Relationship of daily solar radiation values measured at Utah State University Forestry Field Station and at Logan, Utah, May 1 to August 10, 1969.

(Tables 13 and 14). May 4th through May 23rd (D.S.E. 30-49) was characterized by moderate temperatures, high humidity levels and large variation in daily solar radiation levels (Tables 13, 14 and 15). May 24th through June 21st (represented by data during D.S.E. 50-69) was a period of warming temperatures, high daily solar radiation levels with little daily variation and increasing aridity. Due to instrument failure ambient temperature and relative humidity were not recorded during D.S.E. 70-79. End of the season (June 22nd through July 31st, D.S.E. 80-119) was characterized by high daily temperature maximums (greater than 40°C), low relative humidity and maximum solar radiation of little daily variation.

Wind velocity was low during the morning hours throughout the season (Table 16). Winds during the afternoon were always of higher velocity than during the morning hours. Little wind movement occurred during the last hour or two of the day. Mean wind velocities during each hour after D.S.E. 80 were higher than those of previous periods.

In addition to the daily and seasonal variation in abiotic factors a difference in these factors was also observed between the three habitat types (the lawn, field and sage). Little difference was observed in relative humidity levels for the three habitats during D.S.E. 10-49 (Table 14). After D.S.E. 50, the relative humidity levels of the field and sage were usually 20-30 percentage points below that recorded on the lawn. The high humidity levels of the lawn after D.S.E. 50 reflected the artificial watering of this area. Few differences were noted in the mean hourly relative humidity levels of the field and sage for any given daily period.

Table 13. Mean hourly temperature °C at 2 cm above the ground in the lawn, nonlawn open and sage of 10-day periods during the 1970 season (April 14-August 15) at Utah State University Forestry Field Station.

		Hour of the day													
D.S.E.	Habitat	6	7	8	9	10	11	12	13	14	15	16	17	18	19
10-19	L.			-3	1	3	4	5	6	6	1				
	N.L.				3	3	2	6	5	3	4				
	S.				3	3	2	6	4	2	4				
20-29	L.		1	1	5	7	11	10	17	15	16	22	7		
	N.L.		3	5	8	9	11	10	18	18	15	9	1		
	S.		2	3	7	9	9	7	19	17	13	9	1		
30-39	L.		10	16	20	28	28	26	26	28	30	34	29	23	
	N.L.	5	8	18	22	23	26	26	26	16	20	19	14		
	S.	6	8	15	20	21	25	26	23	20	15	15	13		
40-49	L.	6	10	15	21	22	24	25	21	21	20	28	23	19	
	N.L.	4	10	16	19	22	24	26	27	27	27	25	23	21	
	S.	-	7	14	16	24	35	33	30	29	28	24	20	18	
50-59	L.	5	9	13	18	21	21	22	29	17	14	12	14	11	
	N.L.	6	11	16	26	25	27	25	27	34	22	31	28	11	
	S.	5	9	14	20	23	20	26	26	29	25	20	16	12	
60-69	L.	6	12	21	23	28	29	30	31	34	32	29	28	20	13
	N.L.	6	8	14	20	29	30	31	31	30	30	30	30	20	15
	S.	5	8	18	20	26	24	27	27	29	29	24	25	20	15
80-89	L.	6	13	18	23	23	28	32	39	43	44	40	33	26	17
	N.L.	5	16	24	31	34	35	37	37	37	34	38	35	25	20
	S.	5	8	18	24	29	33	33	33	33	30	31	28	26	20
90-99	L.	8	17	24	29	30	32	31	31	32	33	32	33	27	18
	N.L.	5	13	23	28	33	40	41	42	40	38	37	36	29	21
	S.	6	11	18	25	30	34	34	31	30	26	24	29	23	23
100-109	L.	5	7	18	23	30	35	37	35	39	45	38	33	28	18
	N.L.	7	10	22	28	35	44	42	41	44	41	30	22	21	18
	S.	4	9	19	27	33	34	35	36	36	38	33	22	21	13
110-119	L.	6	10	17	27	30	28	30	29	31	34	35	31	27	17
	N.L.	3	11	19	25	32	33	33	24	34	34	34	31	28	15
	S.	2	5	13	19	27	27	32	32	33	31	28	27	26	15
120-129	L.	4	6	14	21	29	34	37	29	25	35	34	30	24	17
	N.L.	9	14	23	30	35	36	35	40	42	39	40	39	32	20
	S.	9	12	20	28	30	30	34	38	38	36	34	34	27	19
130-139	L.		7	19	26	32	42	38	40	40	36	30	27	25	18
	N.L.		16	25	31	38	40	42	44	45	44	42	42	36	25
	S.		16	19	23	28	30	33	33	35	35	35	34	30	20

L. = Lawn
N.L. = Field
S. = Sage

Table 14. Mean hourly relative humidity at 2 cm above the ground in the lawn, nonlawn open and sage of 10-day periods during the 1970 season (April 14-August 15) at Utah State University Forestry Field Station.

		Hour of the Day													
D.S.E.	Habitat	6	7	8	9	10	11	12	13	14	15	16	17	18	19
10-19	L.			100	85	80	80	70	70	70	100				
	N.L.				70	80	75	55	60	60	65				
	S.				50	65	90	70	65	70	70				
20-29	L.		90	90	75	60	50	50	50	55	55	65	80		
	N.L.		50	65	70	65	50	50	40	45	40	50	75		
	S.		50	65	50	45	50	65	45	45	50	50	75		
30-39	L.		90	85	85	80	75	75	70	80	85	85			
	N.L.		80	80	75	80	65	60	55	60	65	75			
	S.		80	85	85	80	70	70	65	70	70	70			
40-49	L.	90	90	85	80	70	65	60	60	55	50	65	70	75	
	N.L.	60	55	50	40	45	35	40	40	35	35	40	50	55	
	S.	65	60	55	50	45	40	40	35	35	30	35	55	60	
50-59	L.	75	75	75	75	80	80	75	45	50	40	45	40	40	
	N.L.	40	35	30	20	25	25	20	25	25	20	20	20	35	
	S.	40	35	25	25	30	25	25	25	20	20	20	25	25	
60-69	L.	70	65	50	45	30	20	30	--	20	30	--	--	--	
	N.L.	60	60	50	40	40	45	35	35	35	35	35	--	--	
	S.	70	55	55	50	40	40	40	--	40	40	--	--	--	
80-89	L.	70	75	85	90	90	60	60	80	50	50	45	55	55	60
	N.L.	75	65	50	40	35	35	30	25	25	25	25	30	35	45
	S.	75	65	60	55	45	40	40	40	35	35	35	35	40	50
90-99	L.	70	90	80	80	85	95	90	80	60	60	60	55	65	75
	N.L.	70	75	75	75	60	55	35	30	25	25	25	25	35	45
	S.	60	80	80	65	60	45	40	40	40	40	40	35	45	45
100-109	L.	85	95	100	80	70	60	50	70	80	100	40	50	45	65
	N.L.	65	70	55	40	35	25	25	35	40	35	35	40	40	50
	S.	65	80	70	70	50	35	30	25	25	35	30	35	45	60
110-119	L.	85	95	100	80	70	60	50	45	45	40	40	50	45	65
	N.L.	75	70	70	65	60	50	40	25	25	30	30	30	35	45
	S.	80	80	75	65	50	35	35	35	30	30	30	35	35	50
120-129	L.	60	70	60	60	55	55	55	55	55	55	45	55	35	60
	N.L.	60	70	60	45	35	30	25	25	25	25	25	20	20	30
	S.	55	60	55	50	35	35	25	30	35	35	35	30	30	50
130-139	L.	65	60	50	45	25	35	30	30	25	35	45	35	31	55
	N.L.		40	40	35	30	25	20	15	--	--	10	15	15	
	S.		45	55	40	30	25	20	20	--	--	10	20	20	

L. = Lawn
N.L. = Field
S. = Sage

Table 15. Mean and standard deviation of daily solar radiation (cal/cm^2/day) at Logan, Utah, April-August (D.S.E. 0-130), 1970.

	D.S.E.			
	0-29	30-49	50-79	80-130
Mean	446.77	535.47	535.47	642.87
Standard Deviation	148.49	176.82	134.6	95.3
Sample	30	19	29	54

Table 16. Estimated season mean and standard deviation of wind velocity (Beaufort scale) during two-hour periods of the day, April 4-August 15, 1970, Utah State University Forestry Field Station.

	Hour Periods						
	6-7	8-9	10-11	12-13	14-15	16-17	18-19
Mean	0.38	0.73	2.80	3.85	4.06	4.15	1.66
Standard Deviation	.52	.50	1.33	1.38	.72	.93	1.27
Sample	24	24	23	22	20	24	24

Little variation was noted in hourly temperature between habitats during the first 59 days of the season (Table 13). Thereafter, the sage community was generally cooler by 2-5°C than the lawn or field. The exceptions were the first and last hours of the day when temperatures were similar for all habitats. The field appeared to be the most severe habitat in terms of amplitude of daily temperatures. After D.S.E. 80, the maximum daily temperature in the field was consistently higher than 40°C. Daily variations were as high as 37°C in six hours. In contrast the maximum daily temperature of the lawn was normally less than 40°C. The lawn was watered until D.S.E. 110-119. The evaporative cooling of the lawn undoubtedly contributed to this difference in daily temperature maximums.

Temperatures within active burrows of the lawn and field were measured after D.S.E. 40 (Table 17). During the period D.S.E. 40-59, mean daily temperatures of all burrows were about 10°C. After D.S.E. 60, average diurnal temperatures within burrows increased 1-3°C each 10-day interval. Differences in the diurnal stability of burrow temperatures in the lawn and field were also noted after D.S.E. 60. Although average temperatures within burrows of the lawn increased with season, and differences were observed between burrows of the lawn, little diurnal variation was observed in individual burrows. Temperatures in burrows of the field, however, were characterized by observable diurnal variation and temperatures normally higher than those in the lawn after D.S.E. 69 (Table 17). The diurnal variation of temperatures in a burrow of the field are illustrated by data taken during D.S.E. 96. The burrow temperature at 06:16

Table 17. Mean burrow temperatures °C of burrows in the lawn and nonlawn D.S.E. 40-129, 1970, Utah State University Forestry Field Station.

	Nonlawn						Lawn		
	Morning			Afternoon			Day		
D.S.E.	X	S.D.	N	X	S.D.	N	X	S.D.	N
40-49	(10)	(.63)	(12)	(12)			8	0.0	12
50-59	13.1	.59	6	6	13.2	7	10.2	.58	16
60-69	15.1	0.0	4	4	15.3	6	13.4	.31	15
80-89	13.2	1.7	7	7	16.4	11	15.4	.37	11
90-99	17.7	0.76	5	5	20.5	11	16.2	.78	15
100-109	16.5	0.0	6	6	22.3	5	16.8	1.52	17
110-119	17.1	2.59	7	7	22.4	9	17.9	.11	15
120-129	20.0	0.89	7	7	19.2	8	18.3	.36	16

( ) = Daily mean

hours was 17.5°C, at 12:00 hours was 20.5°C, at 19:00 hours was 26°C and at 19:45 hours was 25°C. No record of temperatures exceeding 19°C was made in burrows of the lawn.

The principal factor associated with the higher temperatures and greater diurnal variation of burrow temperatures of the field may have been the difference in soil moisture hence the difference in evaporative cooling at soil surface of the field and lawn. With less water in the soil to evaporate hence dissipate solar heat input, temperatures of the nonlawn were higher and varied more than those of the lawn.

Daily activity patterns

Male and female Uinta ground squirrels differed in their daily activity only during the first 40 days of the season (Table 18). During this 40-day period females had a more or less constant level of activity throughout the day. In contrast, the activity of males increased until the afternoon, decreasing thereafter. As the season progressed, daily activity by both males and females tended to decrease during the midday periods. By the end of the season, activity among males and females was generally restricted to the morning.

These seasonal daily activity patterns are similar to those described for other ground squirrels and other small mammals (Betts 1976, McCarley 1966, Yeaton 1969, Clarkson and Ferguson 1972, Nel and Rautenback 1974).

Table 18. Average hourly activity (percent of hour spent above ground) of male and female ground squirrels during three periods of the 1970 season at Utah State University Forestry Field Station.

Period of the year in D.S.E.	Sex	Period of the Day* 1+	2	3	4	5	# Obs.
0-39	Male	.29	.41	.48	.57	.32	3123
	Female	.26	.19	.20	.22	.22	2587
40-79	Male	.37	.22	.14	.19	.30	2946
	Female	.39	.19	.13	.20	.27	4339
80-119	Male	.31	.14	.8	.9	.15	1416
	Female	.34	.14	.9	.10	.12	1464

Average hourly activity = # obs/hr ÷ (# scans/hr · # target animals/10 day intervals).

* Day is adjusted to a 13 hour day.

\+ 1 = first two hours of the day.
5 = last two hours of the day.
2-4 = Three 3 hour periods representing late morning, noonday and early afternoon respectively.

Environmental abiotics and ground squirrel activity

Influence of each of the measured abiotic parameters on activity was assessed by regressing the hourly activity estimate on the corresponding abiotic mean value. Temperature and solar radiation were treated as though they were independent meteorological variables even though they are not. The activity of male and female ground squirrels was found to be independent of the mean hourly estimates of relative humidity, wind speed and solar radiation for any period of the season. A relationship was, however, observed between the activity estimates of males and females and ambient temperatures (Figures 3-8). Two different activity response curves by squirrels during the season were observed. During April 4- May 13, 1970 (the gestation and breeding periods) activity was either independent of ambient temperature or positively correlated with ambient temperature. Activity of pregnant females was weekly correlated with ambient temperature ($r = 0.22$, $P>.05$, 48 df), but activity by breeding males increased as ambient temperatures increased ($r = 0.36$, $P<.01$, 50 df) (Figures 6 and 3, respectively). After May 13, 1970 (D.S.E. 40) the activity of male and female ground squirrels decreased as ambient temperature increased. As the season progressed and mean daily temperatures became hotter, activity of squirrels became progressively better correlated with ambient temperature ($r = -0.53$ and $r = -0.66$ for females during the lactation and postweaning periods and $r = -0.33$ and $r = -0.51$ for males during the postbreeding and fall periods).

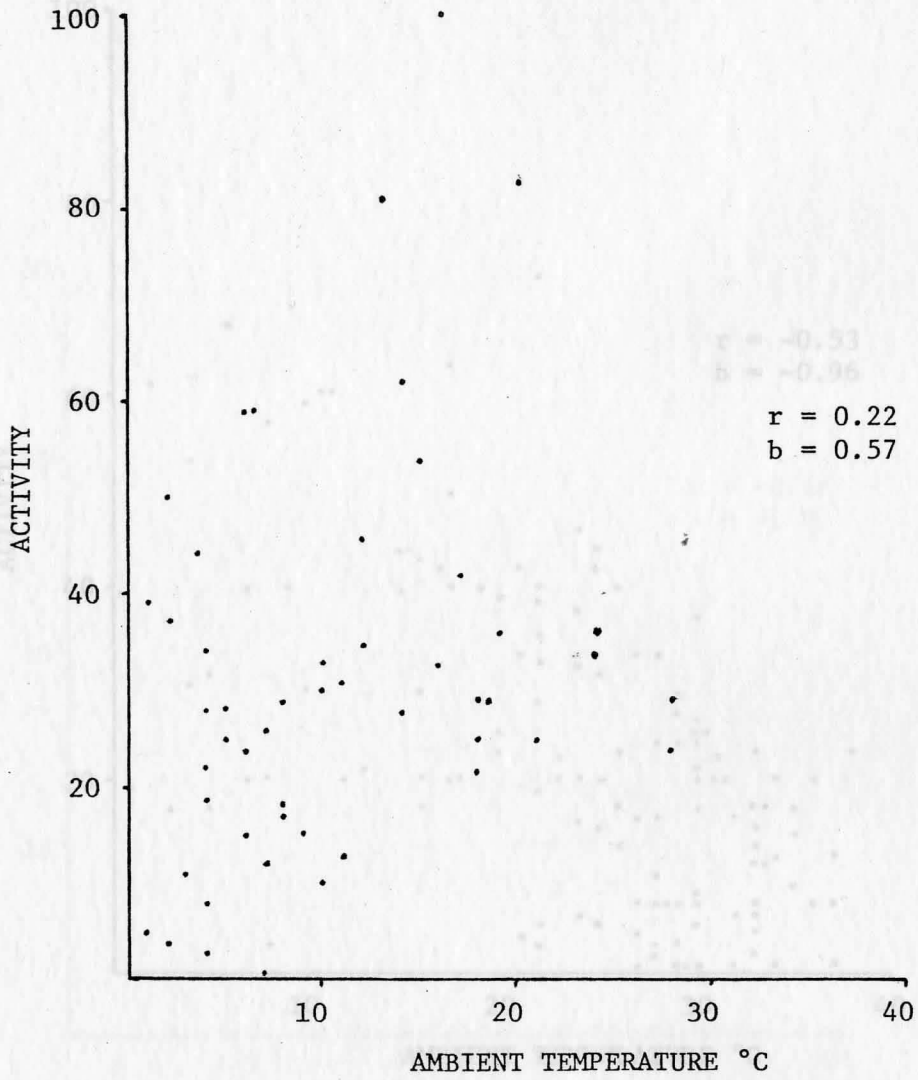

Figure 3. Relationship of activity of mature females and ambient temperature during D.S.E. 10-39, 1970.

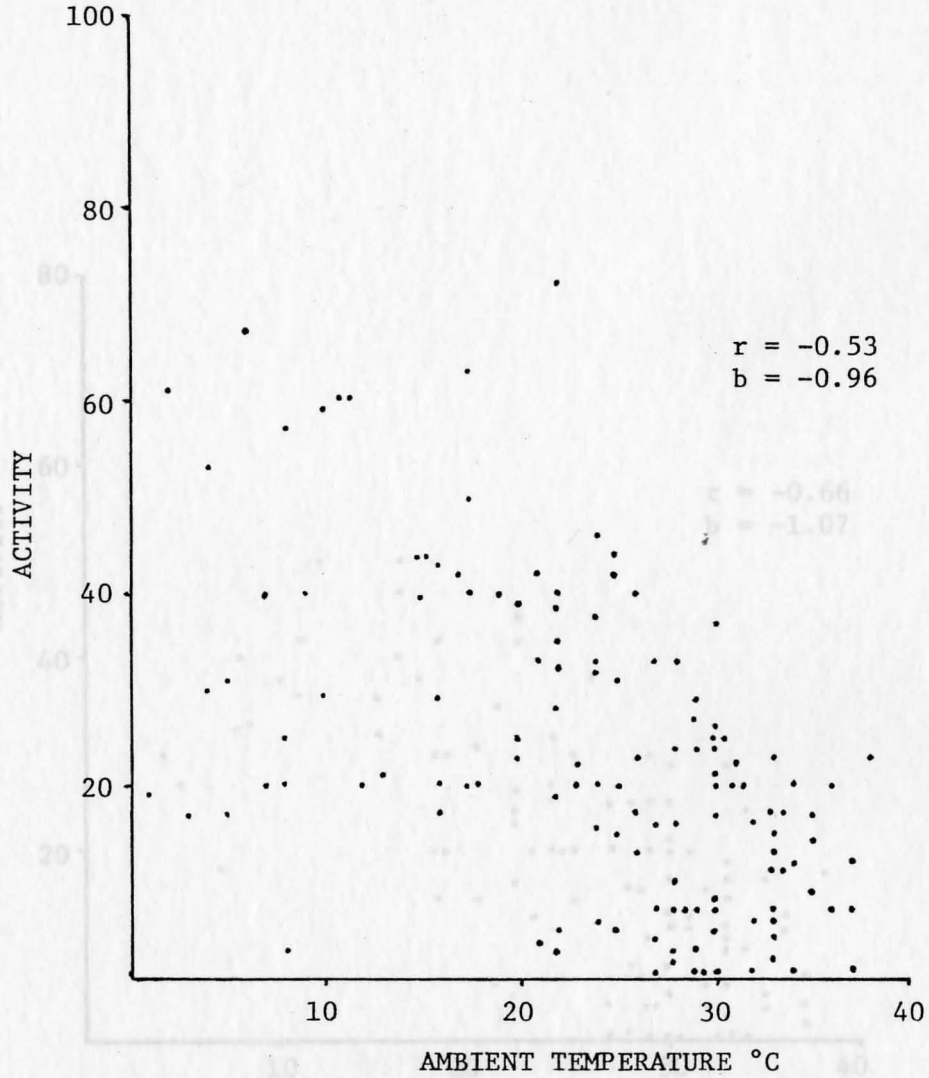

Figure 4. Relationship of activity of mature females and ambient temperature during D.S.E. 40-79, 1970.

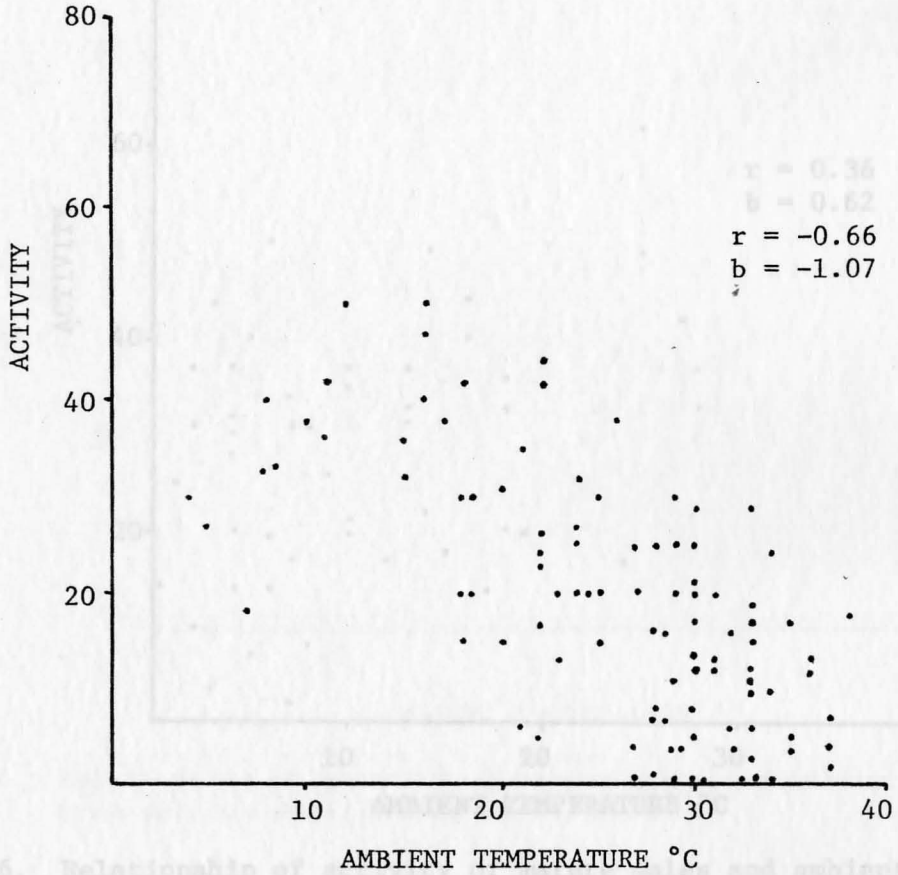

Figure 5. Relationship of activity of mature females and ambient temperature during D.S.E. 80-119, 1970.

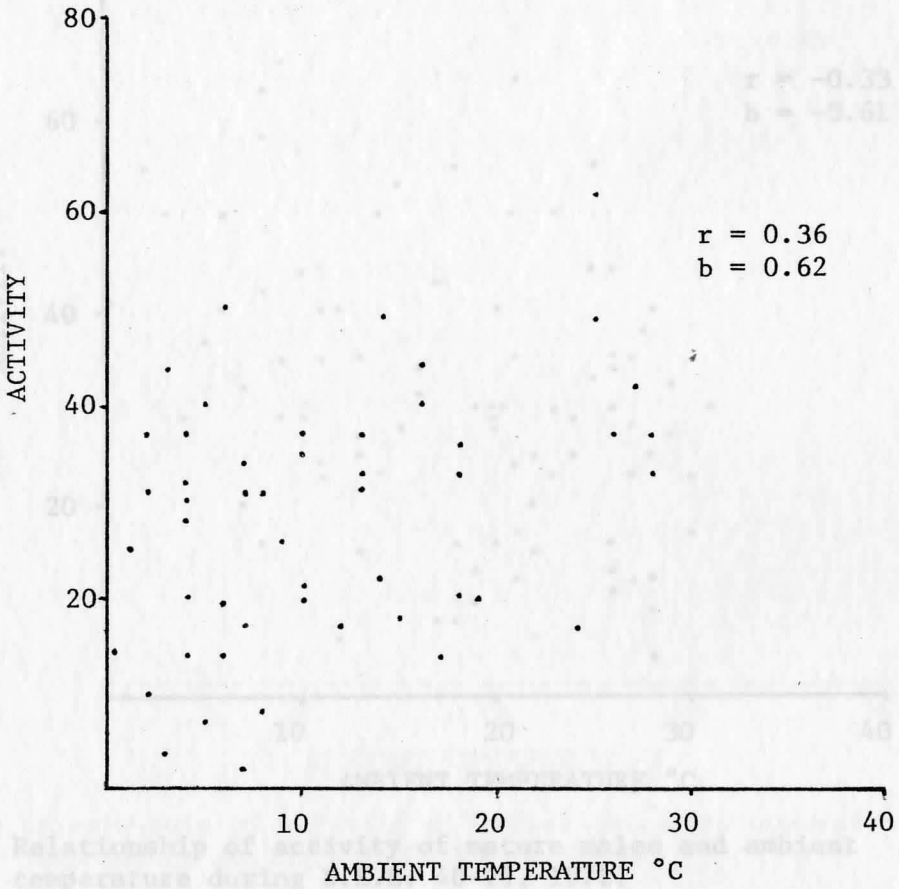

Figure 6. Relationship of activity of mature males and ambient temperature during D.S.E. 10-39, 1970.

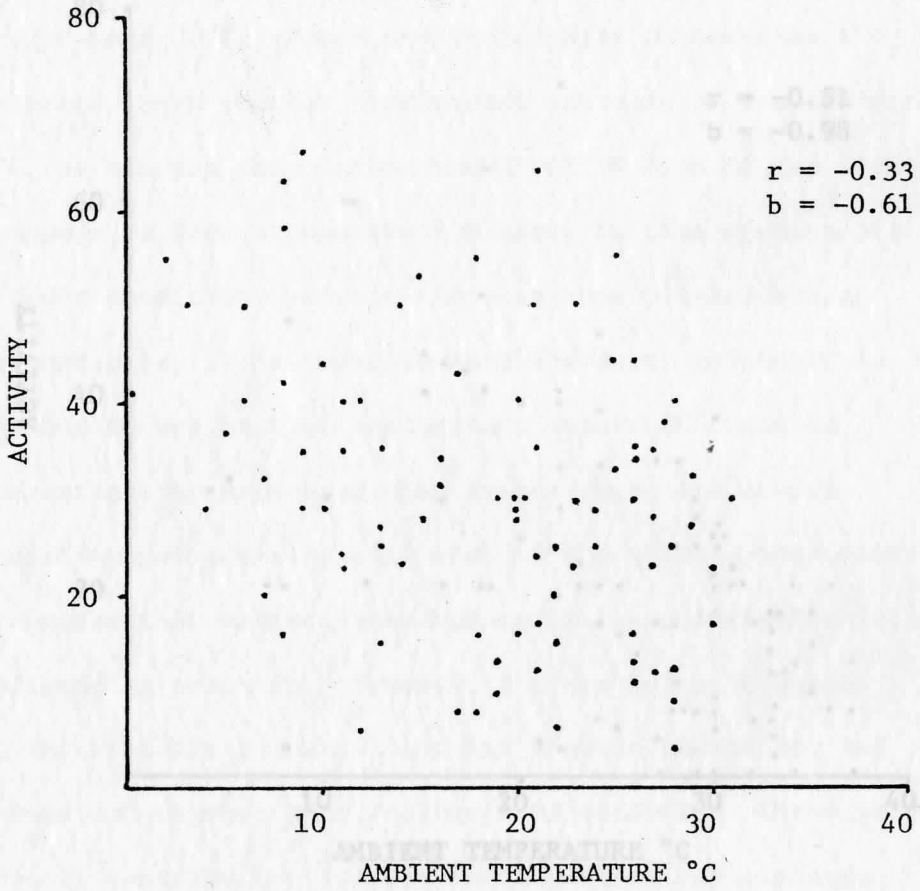

Figure 7. Relationship of activity of mature males and ambient temperature during D.S.E. 40-79, 1970.

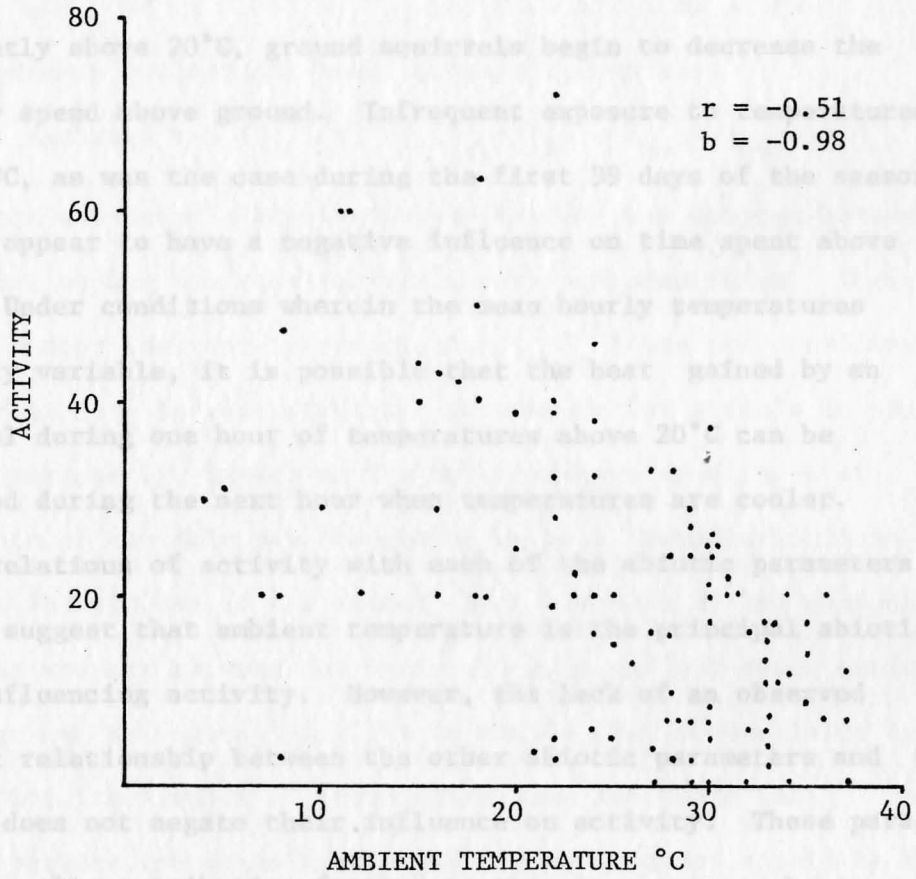

Figure 8. Relationship of activity of mature males and ambient temperature during D.S.E. 70-119, 1970.

It would appear that ground squirrels have an ambient temperature threshold which they cannot be exposed to for long without decreasing activity. When exposed to conditions wherein temperatures are consistently above 20°C, ground squirrels begin to decrease the time they spend above ground. Infrequent exposure to temperatures above 20°C, as was the case during the first 39 days of the season, does not appear to have a negative influence on time spent above ground. Under conditions wherein the mean hourly temperatures are highly variable, it is possible that the heat gained by an individual during one hour of temperatures above 20°C can be dissipated during the next hour when temperatures are cooler.

Correlations of activity with each of the abiotic parameters measured suggest that ambient temperature is the principal abiotic factor influencing activity. However, the lack of an observed dependent relationship between the other abiotic parameters and activity does not negate their influence on activity. These parameters are all contributing factors to the net energy exchange between the animal and its environment. In addition, ambient temperature and solar radiation are dependent meteorological variables. To explore the integrated effect of the abiotic parameters measured, the heat exchange between the animal and its environment was estimated and then correlated with concurrent activity indices.

Environmental heat exchange and ground squirrel activity

I used a modified version of Porter and Gates' (1969) formula to approximate the heat exchange between ground squirrels and their

environment. The heat exchange formula of Porter and Gates as amended by Gessaman (1973, p. 95) for animals in the wild is:

$$M + Q_{abs} = \varepsilon Q T_r^4 + K (V^{1/2}/D^{1/2})(T_r - T_a) + E_{ex} + E_{sw} \pm C \pm W$$

The approximate estimate of heat exchange I used was:

$$\text{Heat exchange} = K (V^{1/2}/D^{1/2}) (T_r - T_a) - E_{ex} + Q_{net}$$

Porter and Gates' term for metabolism (M) was dropped because I could not assume that the squirrels were postabsorptive. Their term for energy loss due to reradiation ($\varepsilon Q T_r^4$) was not considered because this term is very difficult to measure for animals in the wild and because its impact on the heat exchange conditions at the surface of the skin was thought to be low. Reradiation loss occurs at the surface of the animal's fur. Because of low conductivity of the fur and air between the squirrel's skin and the outer surface of the fur and the animal's ability to modify that conductivity by piloerection, the impact of reradiative heat loss upon heat exchange between the animal's skin and its environment should be low. Their term for heat loss due to evaporation of water through the skin (E_{sw}) was dropped because squirrels are not known to sweat. Like Porter and Gates the terms for conductive heat loss (C) and for work (w) were approximated as zero. Thus the approximate estimate I used only incorporates convective heat exchange ($K (V^{1/2}/D^{1/2}) (T_r - T_a)$), evaporative heat loss due to respiratory water loss (E_{ex}) and an estimate of the total solar radiation absorbed by the squirrel (Q_{net}).

The units of the approximated heat exchange were $cal/cm^2/min$. The terms of convective heat exchange were K (a coefficient of

0.00617 cal/m^2), V (wind speed in the open in cm/min), D (diameter of the squirrel's body in cm), T_r (the squirrel's skin temperature) and T_a (the ambient temperature). Diameter of the squirrels was determined by arithmetic manipulation of the estimated surface area of squirrels during each 10-day interval of the season and an average length of 22 cm for males and 20 cm for females. Surface areas were assumed to be a function of body weight and estimated by the surface area formula of Kleiber (1961). Kleiber estimates surface area to be 123.12 cm^2 times body weight in gm to the 2/3 power. Based upon measurements of 10 squirrels taken on a clear day, the surface temperature of squirrels was estimated to be 37°C.

The amount of solar radiation absorbed by the squirrel was assumed to be 70 percent of the incident radiation. Morhardt and Gates (1974) observed a range of solar radiation absorptivity values of 68.9-79.1 percent for the Belding ground squirrel, Spermophilus beldingi, a species similar in pelage color to the Uinta ground squirrel. The amount of surface area exposed to incident radiation at any time was assumed to be 40 percent of total surface area.

Estimation of heat loss due to respiratory water loss was complex. First, Stahl's (1967) predictive formula ($379 \cdot Kg^{0.8}$, where kg is body weight in kilograms) was used to estimate the basal respiratory minute-volume of squirrels. Secondly, it was assumed that respiration rate was correlated with metabolism rate of the ground squirrel. Hudson and Deavers (1973) observed a circadian rhythm of respiration among eight species of ground squirrels (Spermophilus) studied. Data presented by Hudson and Deavers on the spotted ground squirrel, S. spilosoma, and the Richardson ground

squirrel, S. richardsoni, indicated an approximate threefold increase in respiration rates between the lowest (assumed here to approximate basal rate) and that occurring between 0500 hours and 0900 hours (the times the animals normally began their daily activity). Therefore it was assumed that the respiration rate of an active squirrel to be three times the basal rate. Since the metabolism of a lactating female is approximately twice that of a nonlactating female (Kleiber 1961), the respiration rate of lactating females was assumed to be five times the basal rate. Furthermore, it was assumed that above 27°C the respiration rate of wild Uinta ground squirrels followed the pattern of increase demonstrated by Hudson and Deavers (1973, Figure 11) for the Uinta ground squirrel. Finally, the nasal counter-current system was assumed to be 100 percent effective in maintaining the temperature of expired air at ambient temperature. Thus, respiratory water loss was assumed to be a function of the metabolism of the squirrel, the ambient temperature and the saturation deficit between saturated respired air and environmental air. This value was divided by average surface area of the squirrel to estimate heat lost by respiratory water loss per cm^2 per minute.

Heat exchange ($cal/cm^2/min$) of ground squirrels while in the open was estimated and correlated with amount of time spent above ground by each sex during three periods of the season (Figures 9-14). The activity of males was significantly correlated ($P<.01$) with heat exchange during all periods of the season (Figures 9-11). Depending upon the period, 28-35 percent of the variation in time spent above ground by male ground squirrels can be ascribed to the variation in rate of heat gain or loss. In contrast, the amount of

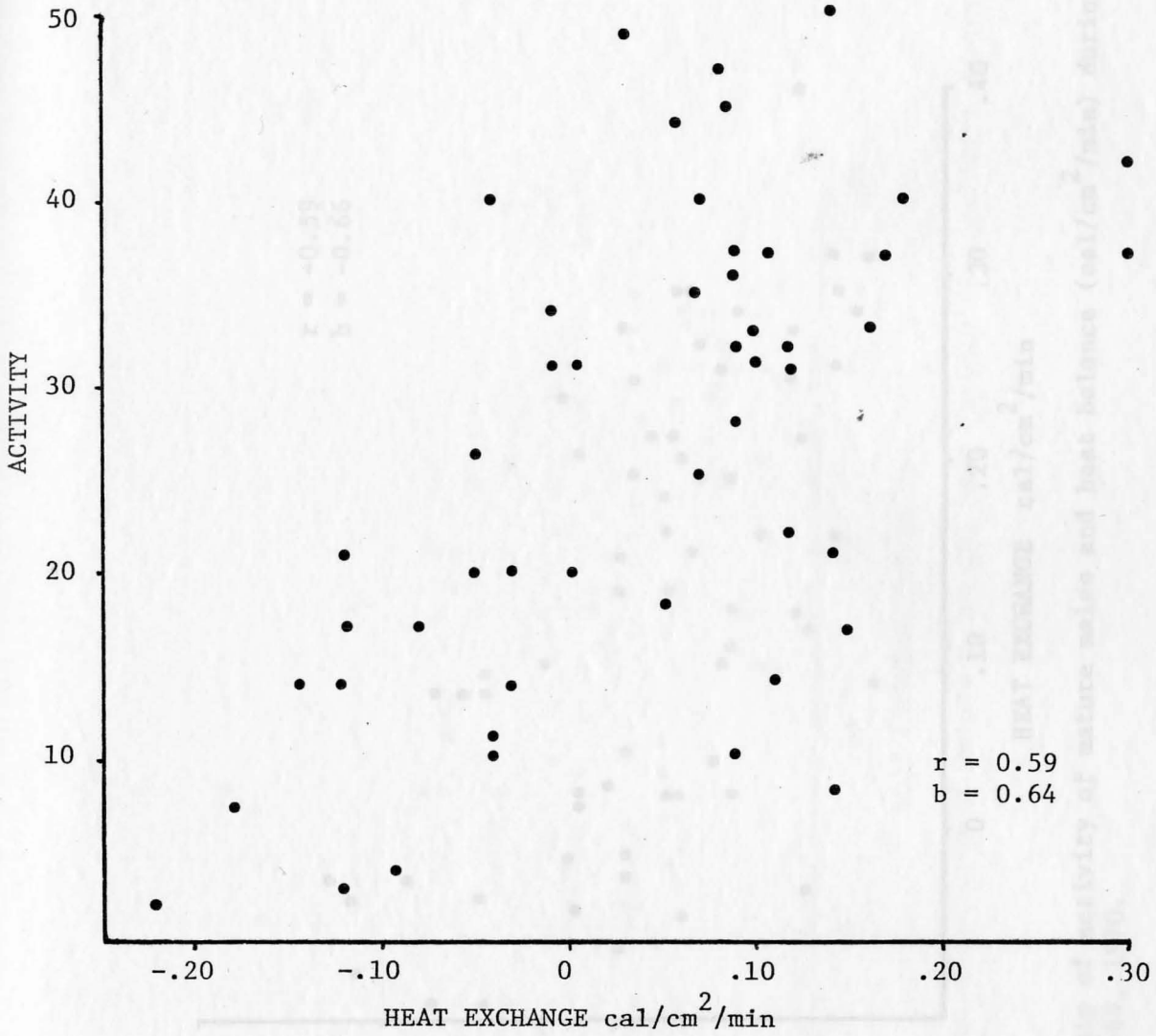

Figure 9. Relationship of activity of mature males and heat balance ($cal/cm^2/min$) during D.S.E. 10-39, 1970.

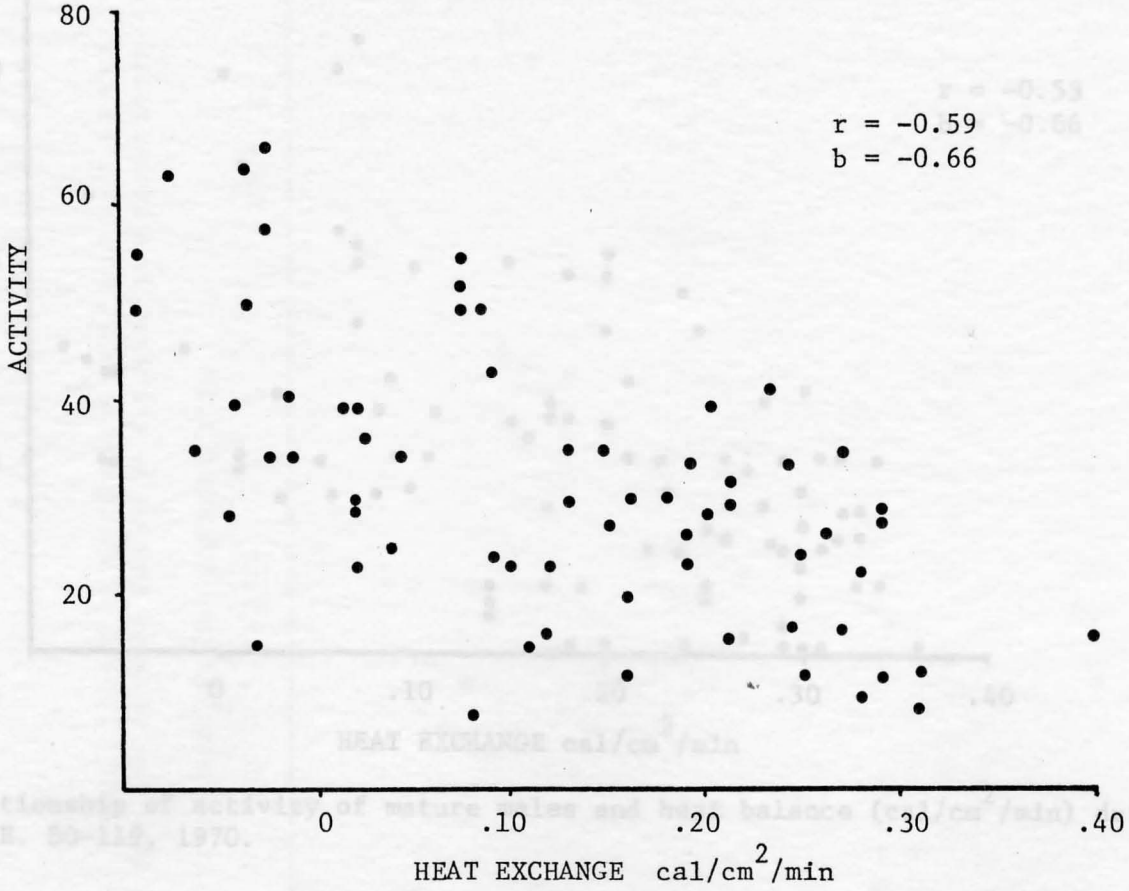

Figure 10. Relationship of activity of mature males and heat balance (cal/cm^2/min) during D.S.E. 40-69, 1970.

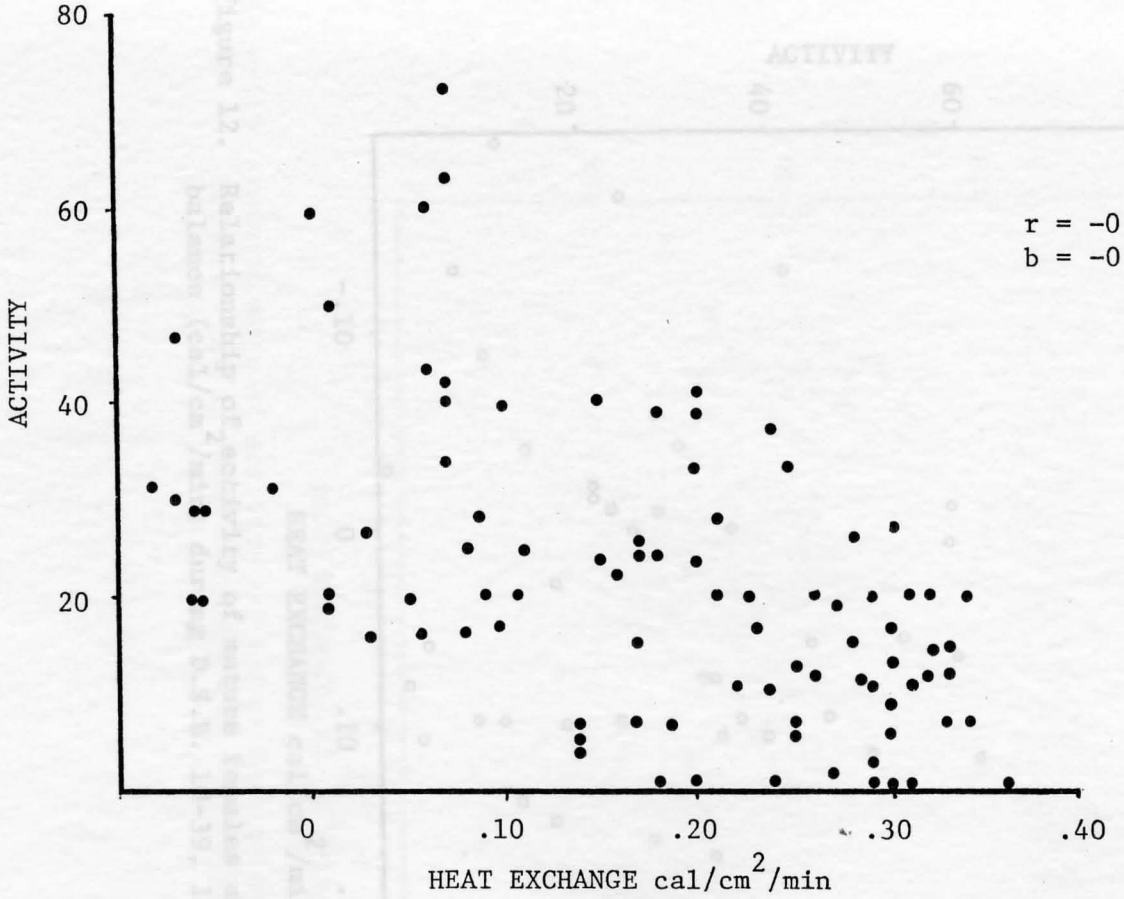

Figure 11. Relationship of activity of mature males and heat balance (cal/cm^2/min) during D.S.E. 80-119, 1970.

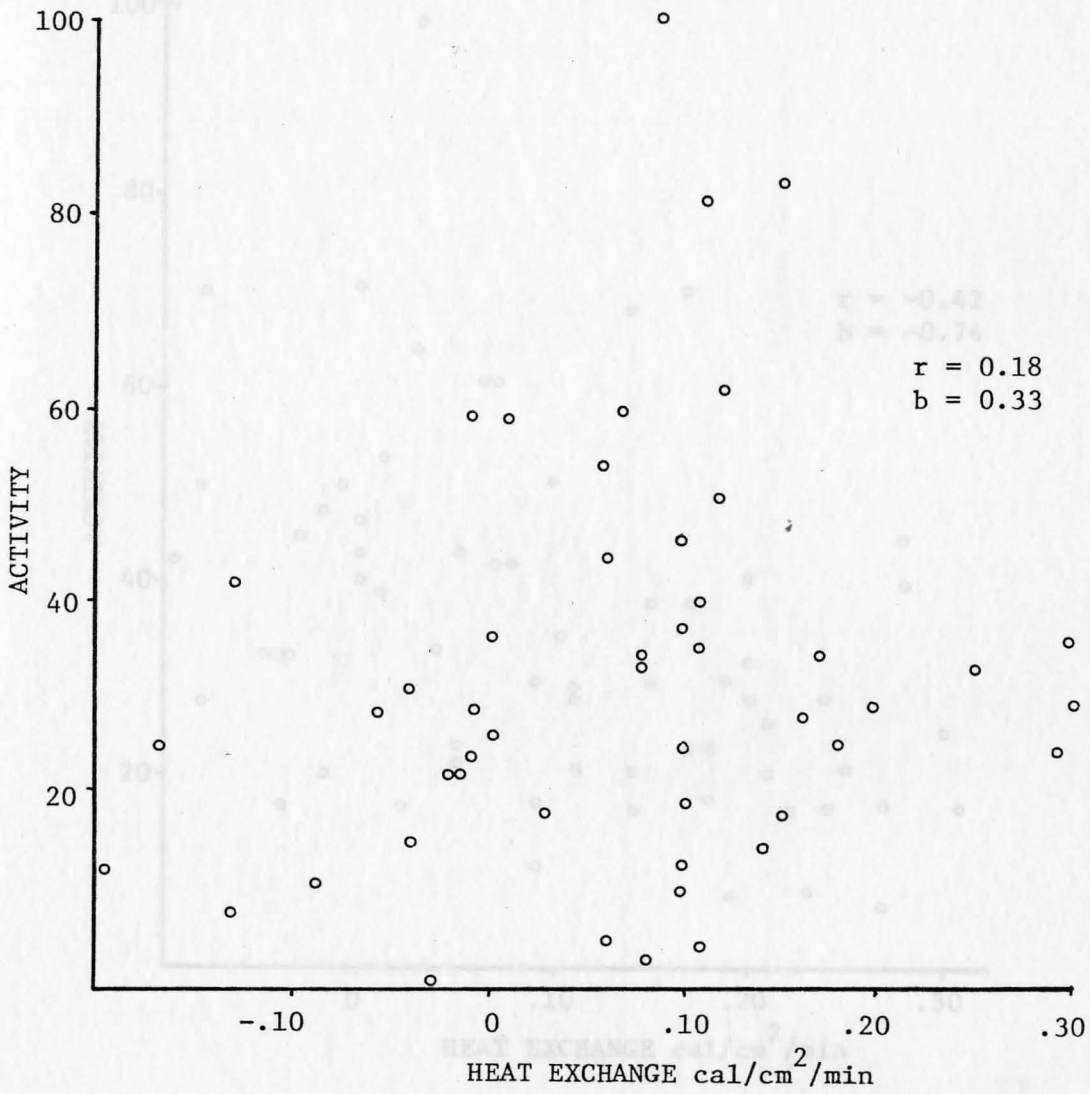

Figure 12. Relationship of activity of mature females and heat balance ($cal/cm^2/min$) during D.S.E. 10-39, 1970.

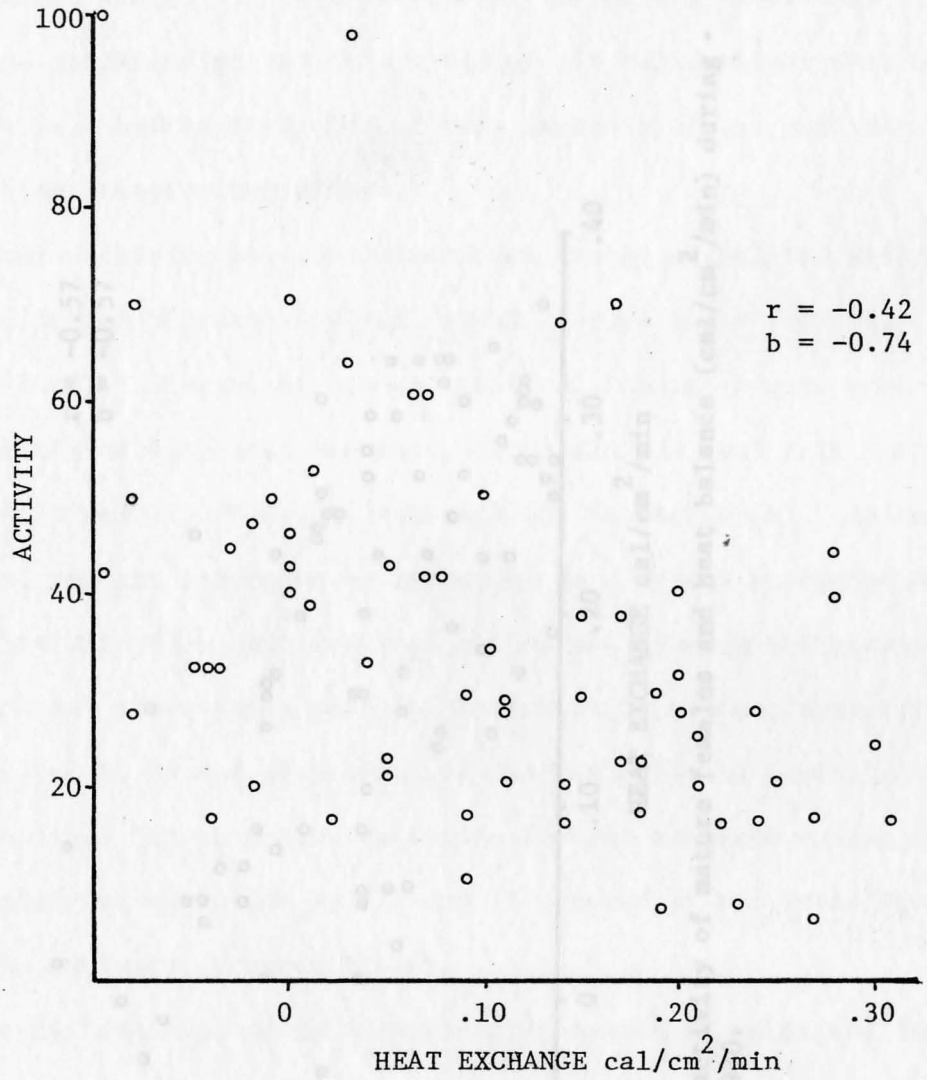

Figure 13. Relationship of activity of mature females and heat balance (cal/cm^2/min) during D.S.E. 40-69, 1970.

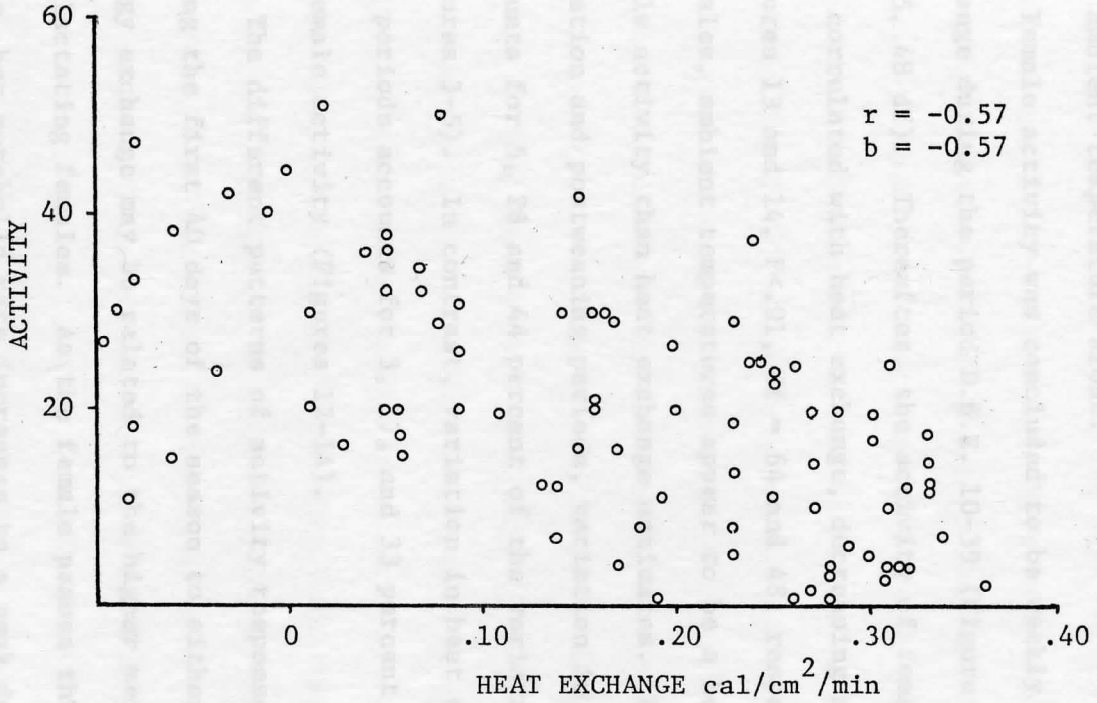

Figure 14. Relationship of activity of mature females and heat balance (cal/cm^2/min) during D.S.E. 80-119, 1970.

variation in time spent above ground due to variation in ambient temperatures was 13, 10, and 26 percent during the respective breeding, postbreeding and fall periods. It would appear that heat exchange is a better predictor of male ground squirrel activity than ambient temperature alone.

Female activity was concluded to be weekly correlated with heat exchange during the period D.S.E. 10-39 (Figure 12, $r = 0.179$, $P<.05$, 48 df). Thereafter, the activity of females became progressively more correlated with heat exchange, decreasing as heat gain increased (Figures 13 and 14, $P<.01$, df = 64 and 48, respectively). In contrast to males, ambient temperatures appear to be a better predictor of female activity than heat exchange estimates. During the gestation, lactation and postweaning periods, variation in ambient temperature accounts for 5, 28 and 44 percent of the variation in female activity (Figures 3-5). In contrast, variation in heat exchange during the same periods accounts for 3, 17, and 33 percent of the variation in female activity (Figures 12-14).

The different patterns of activity response of males and females during the first 40 days of the season to either temperature or energy exchange may be related to the higher metabolism of gestating and lactating females. As the female passes through a reproductive cycle, her metabolic rate increases to a peak during lactation then declines. In heat loss situations, the increased metabolic rate mediates the environmental heat loss potential. In effect, the lower limit of the thermoneutral zone is reduced (Gessaman, personal communication). Thus a pregnant or lactating female is capable of

experiencing heat loss conditions greater than can nonreproducing females before initiating the appropriate physiochemical responses necessary to maintain thermo-equilibrium. In contrast, males do not have the compensatory advantage of above normal metabolic activity. In addition, they tend to feed less than females during the first 40 days of the season (Table 6). From an energetic point of view, it would be advantageous for males to avoid heat loss situations, particularly when the animals may be relying upon its fat reserves as the principal source of metabolizable energy.

After D.S.E. 40, activity among males and females was generally restricted to the morning and evening hours when heat loss or gain between the animals and its environment was low. It would appear the primary thermoregulatory problem after D.S.E. 40 was mediating the rate of heat gain while above ground.

As we saw in the correlation of squirrel activity and ambient temperature there were two different activity curves during the season. During the first 39 days when heat loss was common, squirrel activity was independent or positively correlated with heat gain. Thereafter, when conditions of heat gain were common and of high value, activity of squirrels decreased as heat gain increased.

Heat exchange in and use of alternate environments

The quantity one minus the activity estimate is an index of the time squirrels spent at locations other than in the open. These locations are the burrow systems and the areas covered by tall vegetation. In many instances, particularly during the latter

portion of the season, more than 50 percent of an hour was spent in these environments (Figures 11 and 14). It is therefore of interest to estimate the heat exchange between a squirrel and these environments.

The burrow system of the ground squirrel is structurally simple. Its composition is a few passageways and a nest site. Most passageways and the nest during the homeothermic season are within 35 cm of the surface (D. Balph, personal communication). The hibernaculum sites are usually within 80 cm. Since the exact depth of the nest site was not known, I assumed two conditions in estimating the soil temperature about the nest (Table 19). In the first condition I assumed that the soil temperature about the nest was constant at 6°C (measurements taken in early 1973, Gessaman, personal communication). At a soil temperature of 6°C, the insulating characteristics of the nest resulted in an effective nest temperature of 18°C while the ground squirrel was occupying the nest (Gessaman, personal communication). The second condition I assumed was that soil temperature about the nest was the same as the observed passageway temperatures. Effective temperatures of the nest with soil temperatures above 6°C were estimated by assuming that the effective nest temperature at any burrow temperature was determined by the ratio Gessaman observed (6:18).

The heat loss ($cal/cm^2/min$) of ground squirrels while in the nest and in burrow passageways was estimated for burrow systems in the lawn and nonlawn (field) habitats (Table 19). Rate of heat loss by an animal in the burrow system decreased as the season advanced. At end of season, rate of heat loss in the burrow system was approximately one-half the rate at the beginning of the season.

After D.S.E. 59 temperatures in the passageways of burrows in the nonlawn began to vary with time of day. During D.S.E. 110-119

Table 19. Estimated heat loss (cal/cm^2/min) of mature Uinta ground squirrels while in the nest and in burrow passageways D.S.E. 10-119, 1970, Utah State University Forestry Field Station.

D.S.E.	Stable Nest (T * at 18° C)		Unstable Nest Nonlawn					Burrow Nonlawn					Unstable Nest Lawn			Burrow Lawn		
			Male		Female			Male		Female								
	Males	Females	M.	A.	M.	A.	Te	M.	A.	M.	A.	Ta	Male	Female	Te	Male	Female	Ta
10-19	.08	.09	(.08)+		(.09)		18	(.14)		(.15)		6@	.08	.09	18	.14	.15	6
20-29	.08	.08	(.08)		(.09)		18.6	(.14)		(.13)		7	.08	.09	18.6	.14	.13	7
30-39	.07	.07	(.07)		(.07)		20	(.11)		(.11)		9	.07	.07	19	.11	.11	8
40-49	.07	.07	(.07)		(.06)		20	(.10)		(.11)		10	.06	.07	20	.11	.11	9
50-59	.08	.08	(.06)		(.06)		22	(.10)		(.10)		13	.07	.07	20	.11	.12	10
60-69	.07	.08	.06	.05	.06	.05	22/24	(.09)		.10	.09	13/15	.06	.07	22	.09	.10	13
80-89	.07	.08	.06	.05	.06	.05	22/24	.08	.07	.10	.09	13/16	.05	.06	24	.08	.09	15
90-99	.06	.08	.04	.03	.05	.04	25/27	.07	.06	.08	.07	17/20	.04	.05	24	.07	.08	16
100-109	.06	.06	.04	.03	.05	.03	24/28	.07	.05	.08	.06	16/22	.04	.05	25	.07	.08	17
110-119	.06	.07	.04	.03	.05	.04	25/28	.07	.05	.08	.06	17/22	.04	.05	25	.06	.07	18

* = Effective ambient temperature.
+ = No difference in morning and afternoon heat loss estimates.
@ = Date from Gessaman, personal communication.

this variation was as much as 6°C between morning and evening. No daily temperature variations were observed in the passageways of burrows in the lawn. Heat loss by a squirrel in the nest was approximately 55 percent of that of an animal in the passageway (Table 19). This reduction, however, depended upon whether or not the soil temperatures about the nest remained stable or varied as passageway temperatures varied. Should the soil temperature about the nest vary as passageway temperatures did, then at the end of the season the heat loss rate of a squirrel in a nest would approximate zero or a heat gain.

Heat exchange of squirrels while in shrub communities were estimated during four periods of the season (Table 20). These periods were D.S.E. 20-29, 50-59, 80-89 and 100-109. These periods represent characteristic abiotic conditions experienced by ground squirrels in the shrub communities during the 1970 season. The heat exchange estimates of animals in shrub areas were compared to concurrent estimates of animals in the open. Due to the difference in incident radiation of the shrub and open areas, heat gain estimates of animals in the shrub areas were approximately 50 percent less than the heat gain estimates of animals in the open (Table 20). Differences in convective heat gain due to lower wind speeds and differences in solar radiation due to canopy cover (Figures 1 and 2) were the principal factors affecting these differences. When ambient temperatures are higher than the individual's surface temperature, high wind speeds result in more of a heat gain than do low wind speeds. By using the shrub areas during periods of heat gain, a squirrel could increase the time spent above ground by

Table 20. Estimates of heat exchange (cal/cm^2/min) of Uinta ground squirrels while in the nonlawn open and in the nonlawn sage communities and in the burrow system during the periods of D.S.E. 20-29, 50-59, 80-89, and 100-109, 1970, Utah State University Forestry Field Station.

	Time of Season															
	20-29				50-59				80-89				100-109			
	Males		Females		Males		Females		Males		Females		Males		Females	
Hour	Sage	Open	Sage	Open	Sage	Open	Sage	Open	Sage	Open	Sage	Open	Sage	Open	Sage	Open
6	-.09	-.03	-.08	-.02	-.12	-.05	-.13	-.10	-.08	-.06	-.06	-.08	-.09	-.07	-.11	-.08
7	-.08	-.01	-.07	.00	-.05	+.01	-.06	.00	-.02	.07	-.04	.05	.00	.07	.01	.05
8	-.07	-.04	-.06	-.03	-	-	-	-	.06	.17	.05	.16	.05	.16	.04	.16
9	-.06	+.00	-.06	+.01	-	-	-	-	.09	.23	.08	.23	.10	.20	.11	.21
10	-.07	-.01	-.07	+.01	.07	.18	.05	.17	.12	.26	.11	.25	.14	.27	.14	.27
11	.03	+.14	+.03	+.15	.07	.19	.05	.17	.14	.30	.14	.30	.14	.29	.14	.29
12	-.17	-.22	-.16	-.20	.10	.21	.08	.20	.15	.30	.15	.31	.15	.31	.15	.32
13	-.07	-.04	-.06	-.04	.05	.15	.04	.14	.14	.31	.14	.31	.15	.30	.15	.31
14	-.05	-.03	-.05	-.02	.04	.16	.03	.15	.12	.29	.12	.28	.13	.28	.13	.27
15	-.11	-.15	-.11	-.13	.06	.16	.05	.15	.12	.27	.12	.27	.00	.06	.00	.05
16	-.14	-.18	-.13	-.17	-	-	-	-	.05	.19	.04	.19	.02	.07	-.01	.06
17					+.02	.09	.01	.07	-.02	.08	-.03	.07	-.01	.02	-.01	.01
18					-.04	.01	-.05	.00	-.04	.02	-.04	.03				
Daily burrow & nest est. of heat balance		S.N.	-.08	-.08		-.08	-.08		-.07		-.08		-.06		-.06	
		U.S.N.	-.08	-.09		-.06	-.06		-.06-.06		-.05-.06		-.03-.04		-.03-.05	
		B	-.14	-.14		-.10	-.10		-.07-.08		-.09-.10		-.05-.07		-.06-.08	

S.N. = Stable Nest Temperatures, U.S.N. = Unstable Nest Temperatures
B = Burrow Temperatures

approximately 100 percent before achieving the same heat load it would gain by occupying an open area.

Qualitative evidence suggests that ground squirrels used the shrub areas more during the latter portion of the annual season than they did earlier. After D.S.E. 60, animals with burrows near tower seven (a nonlawn area adjacent to Logan River) would emerge, remain in the area about their burrows for two to three hours then begin moving into the sagebrush areas. These animals began moving back into the open areas near their burrows in the late afternoon hours. As the season advanced, this pattern of habitat use became more pronounced. After D.S.E. 80, few mature ground squirrels were recorded in the open areas about tower seven during the hours of 09:00 to 16:00. Rather, these animals were last seen in the morning moving toward the riparian growth along Logan River and were observed again in late afternoon returning from these riparian areas. The movement of ground squirrels about tower seven into vegetated areas agrees with the inference derived from Figures 9 through 14. Squirrels were using areas other than the open environments during periods of high heat gains.

Respiratory water loss

Caloric values due to respiratory water loss ranged from 0.0 to 0.03 cal/cm^2/min for females and 0.0 to 0.01 cal/cm^2/min for males during the first 69 days of the 1970 season. Respiratory water loss of squirrels above ground was judged to be an unimportant mode of heat loss during this period. The contributing factors of these low values were high humidity levels and low ambient

temperatures. The relative contribution of respiratory water loss to the heat exchange of an animal increased after D.S.E. 80. The caloric values of respiratory water loss in this period ranged from 0.001 to 0.07 cal/cm^2/min for females and 0.001 to 0.08 cal/cm^2/min for males. The contributing factors were low humidity levels and ambient temperatures above 27°C. As indicated earlier respiratory rate of squirrels is temperature dependent. At temperatures above 27°C, respiratory water loss increases approximately 16 percent with each degree increase in ambient temperature (Hudson and Deavers 1973, Figure 11).

A comparison of the respiratory water loss of male ground squirrels while in the sage, nonlawn open and lawn during D.S.E. 80-119 illustrates the differences in respiratory water loss associated with habitat (Table 21). The differences in respiratory water loss of animals in the lawn and the nonlawn were observed only during the noonday hours. During the morning and evening hours respiratory water loss was similar for animals in all habitats. The higher water content of the lawn soils, due to irrigation, and the transpiration of the lawn are believed to have been the cause of the higher humidity levels of the lawn, hence lower water loss estimates. These differences were much reduced by D.S.E. 100-119, probably due to termination of lawn irrigation. The water loss estimates of squirrels in the sage during the midday were lower (by 15-45 percent) than that estimated for the nonlawn open.

The assumption made in estimating respiratory water loss was that the nasal countercurrent system was 100 percent effective in recovery of the available water of respired air. If the system

Table 21. Estimated heat loss due to respiratory water loss (cal/min) of ground squirrels within habitats during hours of the day during the period D.S.E. 80-119, 1970.

Hour	80-89			90-99		100-109			110-119	
	Sage	Nonlawn	Lawn	Nonlawn	Lawn	Sage	Nonlawn	Lawn	Nonlawn	Lawn
6:00	1	1	1	1	1	1	1	1	2	1
7:00	2	2	2	1	2	1	2	1	3	1
8:00	3	7	3	2	2	2	3	2	4	1
9:00	5	10	3	4	3	9	19	3	5	3
10:00	5	11	3		5	15	28	7	9	5
11:00	19	19	3	29	3	9	36	11	12	9
12:00	15	25	6	26	6	16	39	17		12
13:00	13	27		19	9	29	45	28	16	12
14:00	14	17		12	10	10	8	27	14	10
15:00	14	17		9	10	7	10	23	8	4
16:00	11	14		5	10	4	4	12	6	7
17:00	9	9		9	5	5	5	6	3	6
18:00	5	5		5	3	4	4	4	3	3

Sage = Within the sage community
Nonlawn = Within nonlawn open areas
Lawn = Within lawn open areas

is only 75 or 50 percent effective in recovery of water, then the water losses should be 50 or 100 percent greater than predicted. These differences will not change the seasonal significance of respiratory water loss. Increasing the respiratory water loss by 100 percent would still result in a small contribution to the heat balance of an animal during the period D.S.E. 10-69. During the remainder of the season, an increase in respiratory water loss of 100 percent would result in a large contribution of net heat balance, equivalent to approximately 50 percent of the solar radiation input per cm^2 during the midday period (Table 21). Water losses of this magnitude would probably be expressed by saliva spreading over the head and forelimbs. Saliva spreading or its evidence was never observed in free-living ground squirrels. It was exhibited only by animals in traps after D.S.E. 40.

Behavioral thermoregulation

The thermoregulatory problems faced by a ground squirrel in 1970 were of two extremes. During the first 40 days of the season, periods of potential heat loss were common (Figures 9 and 12). After D.S.E. 40 the opportunities for an animal to incur a heat gain became more common (Figures 10, 11, 13 and 14). From a thermoregulatory point of view the animal must possess effective mechanisms to prevent high heat losses during the spring and mediate rates of heat gain during the summer months. However, most mammals are restricted to their physiological capacities to regulate heat exchange. The physiochemical mechanisms of thermoregulation are appropriate for maintaining a stable body temperature during heat

loss situations but are inappropriate as a mechanism for mediating rate of heat gain in environments of extreme heat (Bartholomew and Dawson 1968). To dissipate heat at ambient temperatures higher than body temperature, animals must work against a gradient of heat flow. Under these conditions the only economical way of maintaining a stable body temperature in a hot environment is by dissipating heat via evaporative water loss. Unless succulent plants or free water are available the animal cannot depend upon evaporative water loss as a long-term means of dissipating heat gain. It is obvious, however, that animals do inhabit environments characterized by periods of intense heat and aridity. Their success in occupying these environments depends upon their ability to "seek out and utilize those special and restricted facets of the total physical environment within which their anatomical and physical attributes can function adequately for survival and reproduction" (Bartholomew and Dawson 1968, p. 398). Thus, the active selection of compensatory microhabitats (behavioral thermoregulation) complement the physiochemical mechanisms to form the animal's total thermoregulatory response to its abiotic environment.

Because the ability to maintain a constant body temperature in a cold environment is less of a challenge to homeotherms than are environments of extreme heat and/or aridity, I assessed the use of compensatory environments (the burrow system) by ground squirrels only for the seasonal period of D.S.E. 40-119 (Figure 15). The assumption made in assessing the compensatory use of a burrow system was that behavioral thermoregulation was the principal mode of maintaining a stable body temperature used by ground squirrels. The

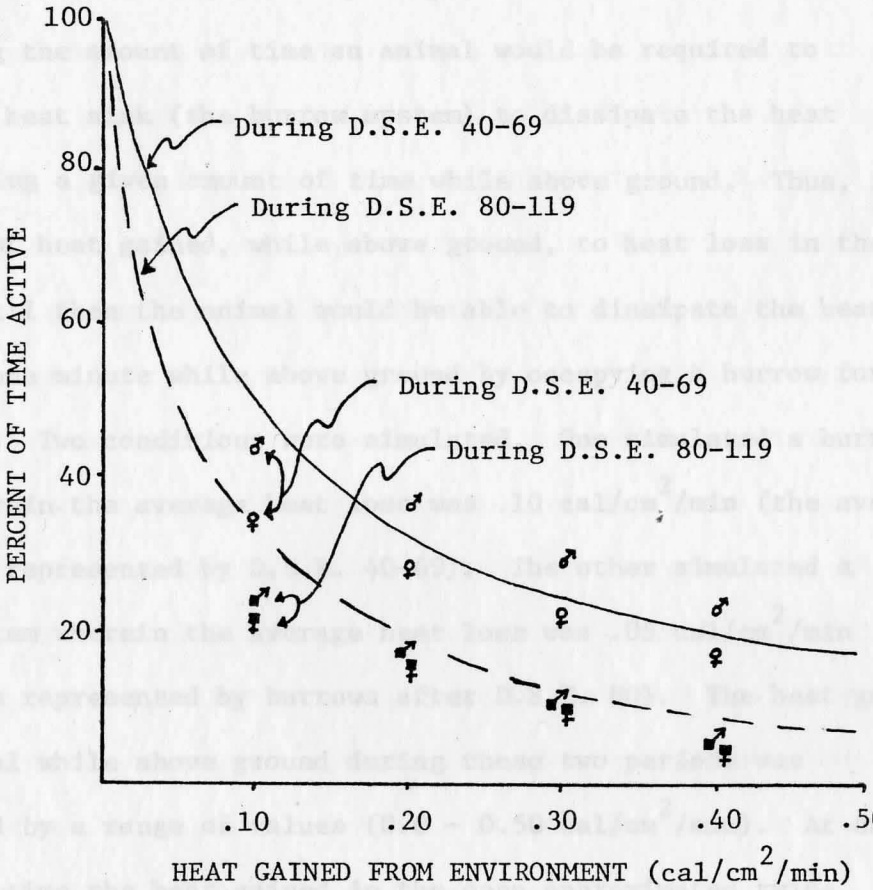

Figure 15. Time ground squirrels would spend above ground if activity were determined solely by behavioral thermoregulation (represented by curves) and the average time spent above ground by male and female ground squirrels (represented by symbols) during D.S.E. 40-69 and 80-119 in 1970. Behavioral thermoregulation is calculated as the time required to occupy the burrow to dissipate the heat gained while above ground. Average amount of time spent above ground by male and female ground squirrels is estimated by the regression line of activity and heat exchange during D.S.E. 40-69 and 80-119 (Figures 10, 11, 13 and 14).

time a squirrel could remain above ground using only behavioral thermoregulation to maintain body temperature was estimated by determining the amount of time an animal would be required to spend in a heat sink (the burrow system) to dissipate the heat gained during a given amount of time while above ground. Thus, if the ratio of heat gained, while above ground, to heat loss in the burrow is 1:1 then the animal would be able to dissipate the heat gained in one minute while above ground by occupying a burrow for one minute. Two conditions were simulated. One simulated a burrow system wherein the average heat loss was .10 cal/cm^2/min (the average conditions represented by D.S.E. 40-69). The other simulated a burrow system wherein the average heat loss was .05 cal/cm^2/min (conditions represented by burrows after D.S.E. 80). The heat gain by an animal while above ground during these two periods was represented by a range of values (0.0 - 0.50 cal/cm^2/min). At any particular time the heat gained in the open approximated twice that experienced by an animal in shrub-brush communities. The plots of the time required to occupy a burrow to dissipate the different rates of heat gained while above ground during the two periods were termed the expected response patterns. To determine if ground squirrels were using behavioral thermoregulation to maintain body temperature, the values of the regression of activity and heat exchange of male and of female ground squirrels during the periods D.S.E. 40-69 and 80-119 (Figures 10, 11, 13 and 14) were plotted and compared with the expected response pattern of each period. The mean values of the correlations of activity and heat exchange

of males and females during the two periods were termed the observed response pattern.

The expected response pattern for conditions similar to those experienced by ground squirrels during D.S.E. 40-69 and 80-119 agrees well with the observed response pattern of squirrels in the open when the rate of heat gain exceeds .15 cal/cm^2/min. Below this level the expected response pattern predicted higher activity than was observed. This lack of agreement below .15 cal/cm^2/min is due to a number of factors. In part the lack of agreement is due to comparing a linear regression relationship (observed) to an exponential relationship (expected). However, I suspect that the main reason is that the time spent above ground by ground squirrels cannot be predicted solely as a function of heat exchange. Where abiotic conditions permit an animal to be above ground for long periods of time, ecological and social factors may preclude the animal spending all of its time above ground.

Body temperatures and the lack of evidence of heat stress in free-living ground squirrels suggest that they are efficient thermoregulators. Body temperatures obtained by telemetry were relatively constant throughout the day (Gessaman, personal communication). Yet the amount of heat required to change body temperature 1°C could be obtained in approximately two minutes during maximum conditions of heat gain (.30 to .40 cal/cm^2/min) after D.S.E. 40. It is unlikely that ground squirrels would rely exclusively upon physiological mechanisms to maintain a body temperature in these situations. Behavioral responses would be more appropriate.

Adaptiveness of behavioral thermoregulation

From an energetic point of view, behavioral thermoregulation should be an important component of total thermoregulation of any homeotherm. The ecological mandates of this adaptation are the daily and seasonal extremes of abiotic conditions associated with any given habitat and the physical heterogeneity of any habitat. Physiological mechanisms of thermoregulation appear to be designed principally for regulation of heat loss. The most effective physiological mechanism of limiting heat gain, and thus maintaining homeothermy, is evaporation of water. Evaporative water loss can be a useful survival method only if environmental water reserves are available to replenish those lost. In general, most small mammals do not use water for evaporative cooling but avoid thermal stress by seeking cool microhabitats (Chew 1965). In situations of potential heat loss, early spring or early morning and late afternoon hours, the physiochemical mechanisms of heat loss reduction can be complemented by postures and body orientation. Due to the availability of both behavioral and physiochemical mechanisms to mediate heat loss, cold environments pose few serious challenges to the ground squirrels homeothermic status. Hence, we tend to observe high activity during these periods.

To a pregnant or lactating female, environments characterized by heat loss may be beneficial, if not required, for peak reproductive success and well-being. The elevated metabolic rate associated with gestation and lactation requires an elevated food consumption rate and an economical means of dissipating larger than

normal heat from the animal. Environments wherein she can obtain the necessary food resources and yet lose heat via convection and conduction would be beneficial. These environments are usually present during the period of April through May at the study area. Females emerging late (mid-May and mid-June) would reach their metabolic peaks 40-50 days later during a period characterized by drying conditions (Sharif 1967) and conditions of high heat gain. The difficulty in dissipating their metabolic heat under these conditions may result in reduced opportunities to feed hence affecting the reproductive performance of the female.

No quantitative data were available on the relationship of high heat gain conditions to reproductive performance among Uinta ground squirrels. However, studies conducted on other mammals indicate a close tie between abiotic factors and reproduction. Among ewes (Ovis aries) reproductive performance is adversely affected by high temperatures, 32-35°C, and favorably affected by low temperatures, 16-21°C (Neville and Nethery 1974). Rats (Rattus spp.) exposed to temperatures of 37°C during the last 14 days of gestation gave birth to smaller than normal young and exhibited lower than normal rates of lactation (Benson and Morris 1971). Other investigators have observed reductions in litter size of rats when females were exposed to a temperature of 35°C throughout gestation (MacFarlane et al. 1957). It is likely that similar responses could be expected of the Uinta ground squirrel if forced to gestate and/or lactate late in the season.

The adaptations that Uinta ground squirrels use to occupy a fluctuating and heterogenous abiotic environments appear to be

mainly behavioral. Three factors contribute to this hypothesis. First, body temperatures are stable at about 38°C with a daily fluctuation of approximately 1.1°C (Gessaman, personal communication). Second, there were no observations of heat stress, saliva spreading or panting among free-living animals, and third, the observed time spent above ground during periods of the season, when conditions of heat gain were common, closely matched a theoretical value computed from heat gain versus heat loss estimates in alternate habitats (Figure 15). Use of microhabitats characterized by heat gain is affected by compensatory use of microhabitats having heat loss characteristics. During periods of high heat gain animals also tended to make greater use of the shrub-covered portions of their environment than of open areas. Furthermore, daily activity is patterned to exploit the periods of heat loss or low heat gain (Table 17).

At the beginning of the season when the thermoregulatory problem is heat loss to the environment, males restricted their time spent above ground to times of heat gain. The time spent above ground by gestating females, presumably due to higher metabolic rates, is independent of the heat exchange estimates. After the abiotic environment stabilized into a predictable pattern of heat gain during the midday bounded by periods of low heat gain, both sexes restricted the time spent above ground to the less stressful periods of the day. These responses conform to the point of view of Bartholomew and Dawson (1968) that animals match their physiological capabilities to physical characteristics of microhabitats. In Uinta ground squirrels these adaptations appear to be refined to the point that physiological capabilities are rarely taxed.

Use of Space

Introduction

The manner in which animals use space has been one of the more complexing subjects of biological investigation. Many biologists assume that use of space is in large part the result of responses to proximate features of the environment and the absence or presence of conspecifics. As such, these responses can be related to 1) social organization, 2) population density, 3) habitat characteristics and 4) energetic requirements of the species (Brown 1975, p. 47, Brown and Orians 1970, McNab 1963, Post 1974 and others).

Because of the difficulties in observing small mammals directly and the need for relatively large numbers of observations on one individual, few behavioral studies of the use-of-space have been conducted on this group. The Uinta ground squirrel is an ideal subject for behavioral study of the use of space. They are relatively large (300-600 gm), acclimate well to the observer, tend to have home ranges of less than a hectare in size, and tend to occupy open habitats (Burns 1968, Walker 1968, Ruff 1971).

The objectives of this portion of the research were 1) to determine the seasonal characteristics of home range size of a sample of male and female ground squirrels, 2) to determine the seasonal dispersion patterns of home ranges of this sample, 3) to determine the influences of effective density upon distribution of behaviors within the home range, 4) to determine the distribution patterns of behaviors within the home ranges of male and female

ground squirrels, and 5) to determine the distribution patterns of aggressive encounters and their results within the home ranges of male and female squirrels.

Methods

The examination of use of space by Uinta ground squirrels was restricted to data collected during the 1970 season. This restriction was made because 1970 was the only year in which numbers of individuals had been observed more than 200 times each during the season. Since the data for each individual were ultimately to be analyzed on the basis of three seasonal time periods and on the basis of how each of eight behaviors was distributed with regard to the distribution of the locations at which each individual was observed in its home range, there was a need to have a large sample size to increase the probability of making correct inferences regarding behavioral use of space by ground squirrels. Nineteen females (12 adults and seven yearlings) and 12 males (seven adults and five yearlings) were observed 200 or more times during the season. Unless otherwise specified, all use of space analysis is restricted to characteristics of these individuals.

The basic spatial reference used in this analysis was home range of the animal. Because observations of squirrels were not continuous, home range of an individual was estimated by the sample of locations within the study area each individual was observed to occupy. Two terms are used throughout this portion of the research. These are a home range locus and home range loci. A home range locus is defined here as any given location at which the individual was

observed. Home range loci are all the locations the squirrel was observed to occupy.

The first problem I had to solve in order to describe the use of space by squirrels was how to define the relative frequency in which a given sector of the home range is used. Other investigators (Calhoun and Casby 1958, Koeppl et al. 1975, Jennrich and Turner 1969 and others) define frequency of home range use by employing a geometric center, a radius and some assumed statistical distribution. The basic variable of these methods is the distance a given home range locus is from the geometric center. The basic assumption of these methods is that use decreases in frequency with distance from the home range center. The main disadvantage of these methods is that the geometric center is an abstraction and the animal may never occupy the area about it (Koeppl et al. 1975). In an attempt to describe more accurately the frequency of home range use, I used the distance a home range locus was from all other loci of the home range to describe frequency of home range use. This method was termed the dispersion index to frequency of home range use. The dispersion index of the "i"th home range locus was determined by the following equation:

$$DI_i = \frac{\sum_{i=1}^{n} \frac{1}{d_{ij}^2 + 1}}{n - 1} \qquad \text{where } i \neq j$$

where $d_{ij}^2 = (X_i - X_j)^2 + (Y_i - Y_j)^2$,

X_i, Y_i = coordinates of the "i"th locus,

X_j, Y_j = coordinates of the "j"th locus,

and n = number of home range loci.

The basic variable of this procedure was the sum of the reciprocal of the square of the distances from the "i"th locus to all other loci of a home range set. When applied sequentially to all the loci of a home range, an array of dispersion indices bounded by scale values of 0.0-1.0 is generated. Those loci with dispersion indices near 0.0 represented the most dispersed loci of a home range and those with values near 1.0 represented the least dispersed (most aggregated) loci of the home range.

This index is scaleless, has no geometric center and assumes no a priori distribution of home range loci. The basic assumption that is made is that the more closely aggregated home range loci are, the greater the use of an area is. Furthermore, it is assumed that the more closely aggregated home range loci are, the more familiar the individual is with that area. Because the behavior of small mammals has been shown to be associated with degree of familiarity they have with a given area (Brown and Orians 1970, Price and Huck 1976, Ruff 1971, Shillito 1963), the index lends itself to analysis of the behavioral use of space.

How a squirrel distributed its behavior in space was the second problem in the analysis of use-of-space. Since behavior of a squirrel was recorded concurrently with location, each time a specific behavior was exhibited within the home range the dispersion index of that location was noted and filed in an array. When the dispersion indices for all the locations at which a specific behavior was exhibited were found, they ranked in order of dispersion index value. The distribution of each behavior within the home range was determined by comparing the ranking of dispersion

indices of a behavior with the ranking of dispersion indices of the home range loci. The Kruskal and Wallis' multisample test for identical populations, sensitive to unequal locations (Bradley 1968, p. 129) was used to determine if the behaviors were distributed differently from the distribution of home range loci.

The use of space and the manner in which specific behaviors were distributed within the home range were determined for each of the 31 animals selected for analysis. These descriptions were made for each of three seasonal periods. Each period represented a reproductive event appropriate to each sex. Since these periods were determined for each individual they are classified as biological time periods. Therefore, between like animals the duration of a seasonal period may vary or be of different calendar time periods. To facilitate description of the use of space by ground squirrels, the dispersion indices of home range loci of each individual were arbitrarily divided into five equal frequency regions. These regions were coded one through five. One represented the most dispersed 20 percent of the loci of the home range and five represented the most aggregated 20 percent of the loci of the home range. Home ranges of each individual were plotted as cells of occupancy. Each cell represented an area 1.22^2 m (4^2 ft). The dispersion index of each cell was coded one through five depending upon its use frequency.

Seasonal changes in home range size and dispersion between home ranges

Home range size and dispersion of home ranges of the 31 squirrels were determined from inspection of the plots of home ranges.

Maps of the home ranges of the 31 squirrels during three periods of the season were drawn (Figures 16-25). Home ranges of these animals are represented by the home range core areas. Core area is defined here as the most aggregated 60 percent of the loci of the home ranges. Core areas were mapped by drawing a connecting line between the outer most cells of the 60 percent most aggregated cells of the home range.

Among males the home ranges during the breeding period were relatively large (Figure 16). During the postbreeding period home ranges were smaller than during the breeding period, and during the fall period home ranges of males increased in size (Figures 17-19). Those males having the largest home ranges were adult males during the breeding period and yearling males during the fall period.

The seasonal pattern of home range size of females (Figures 20-25) differed from that of males. During the gestation period home ranges of females were small, expanding into larger home ranges during the periods of lactation and postweaning.

Associated with the seasonal variation in size of home range among these squirrels was a seasonal variation in dispersion or overlap of core areas of home ranges between these individuals. Among all animals, overlap of the core areas was common during the breeding/gestation and fall/postweaning periods. Conversely, overlap of core areas was less common during the postbreeding/lactation period. The overlap that existed during the postbreeding/lactation period occurred most commonly between core areas of animals of the opposite sex. In general, it appears that the

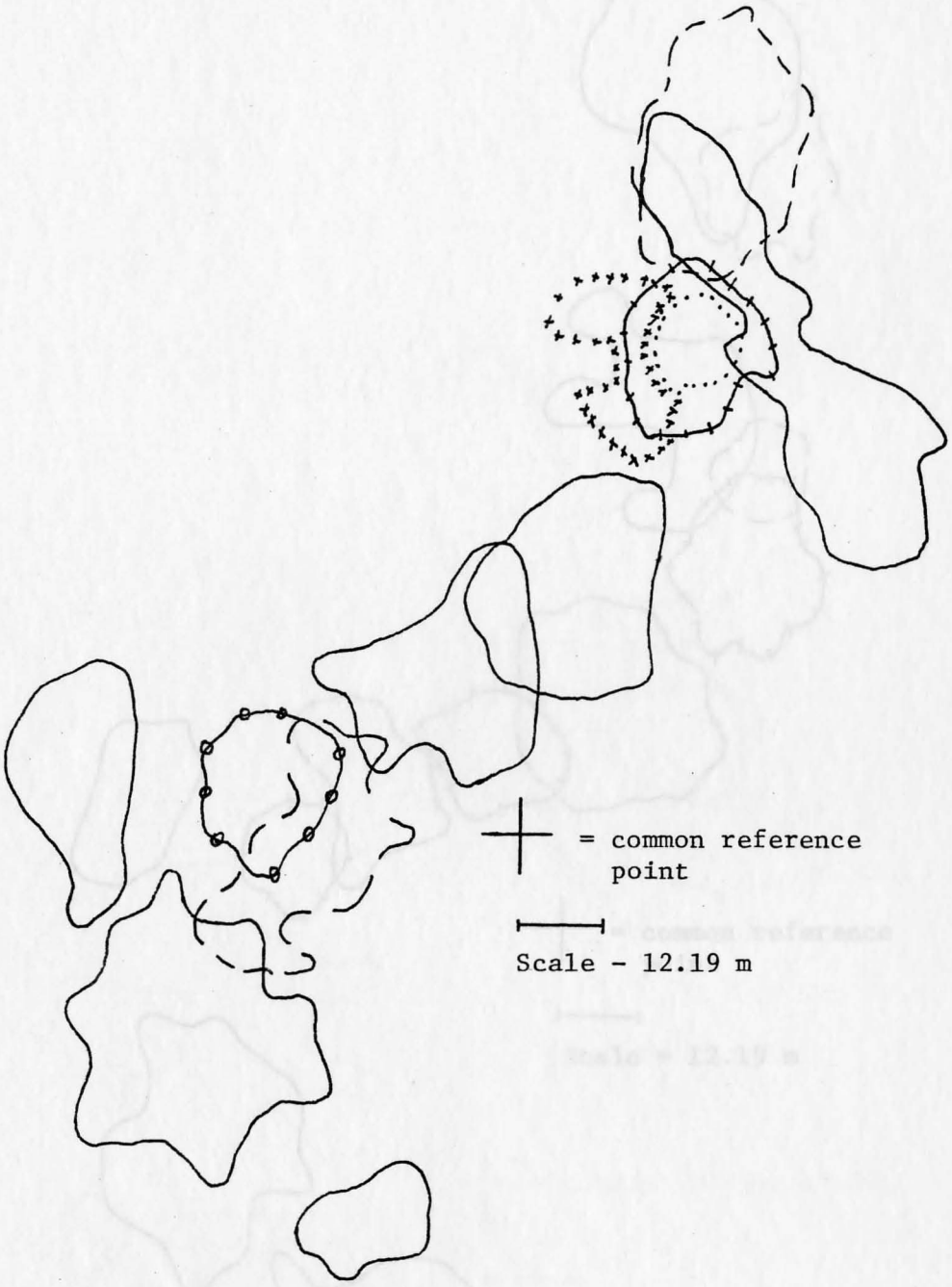

Figure 16. Dispersion of the home ranges of 12 male ground squirrels during the breeding period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

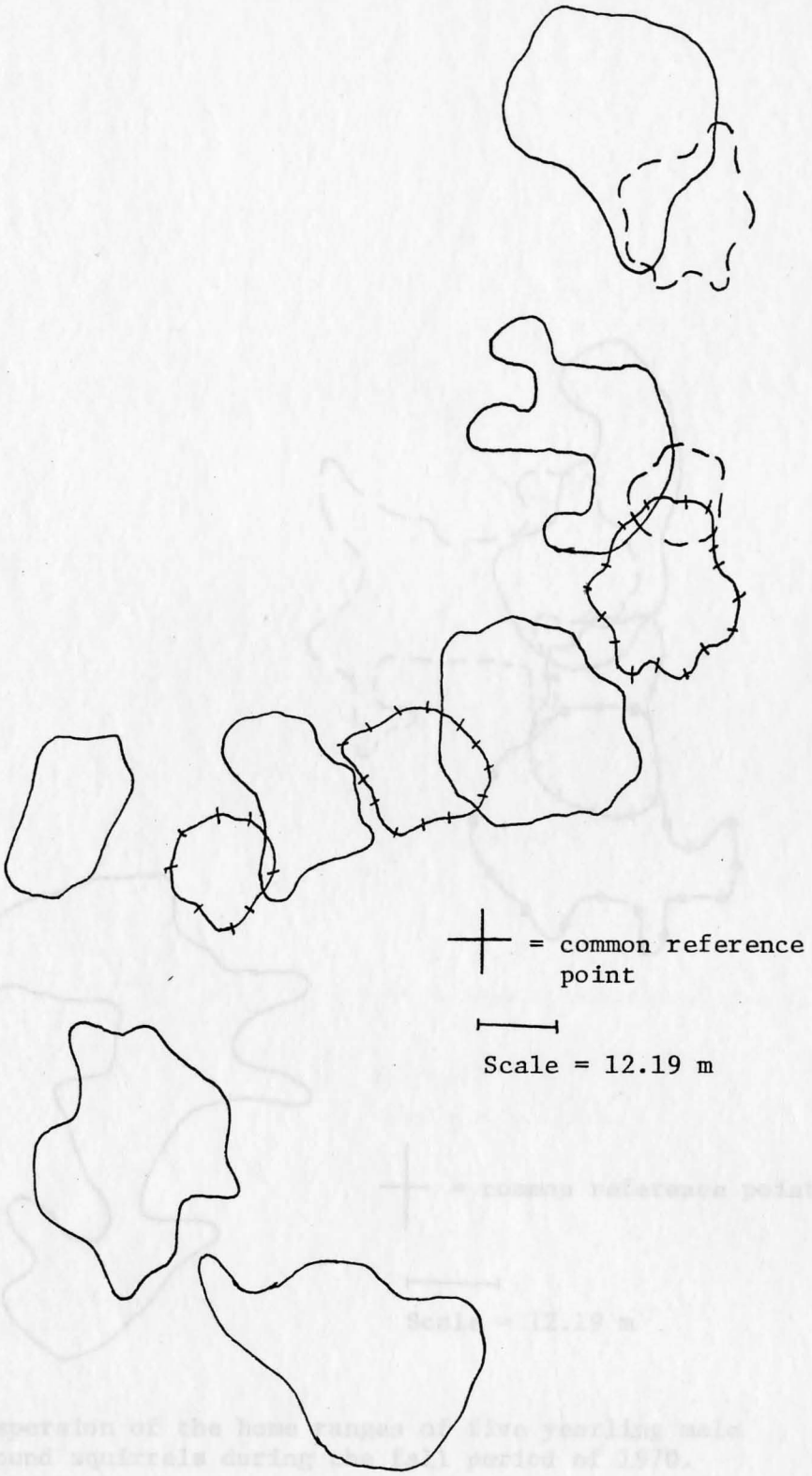

Figure 17. Dispersion of the home ranges of 12 male ground squirrels during the postbreeding period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

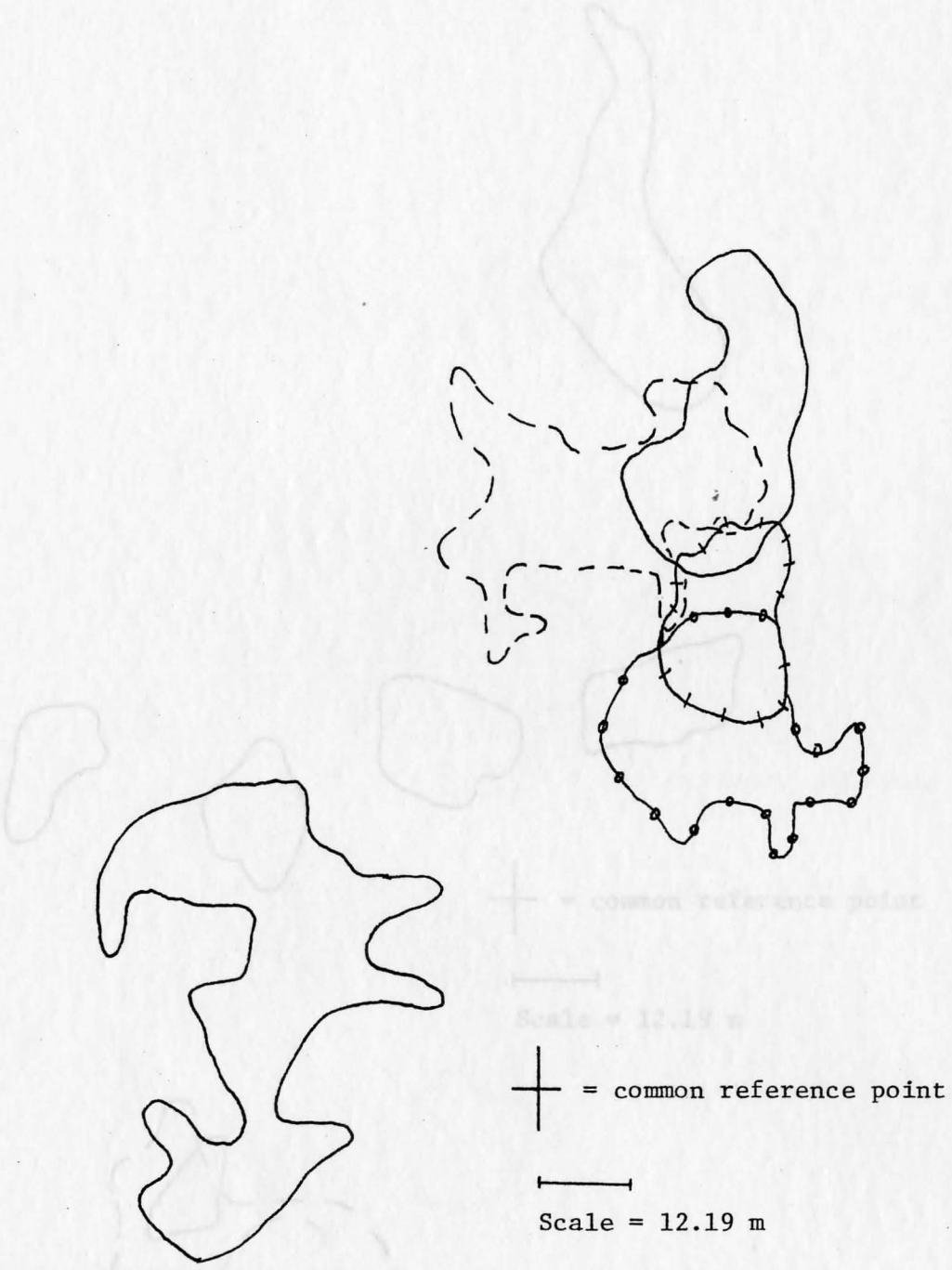

Figure 18. Dispersion of the home ranges of five yearling male ground squirrels during the fall period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

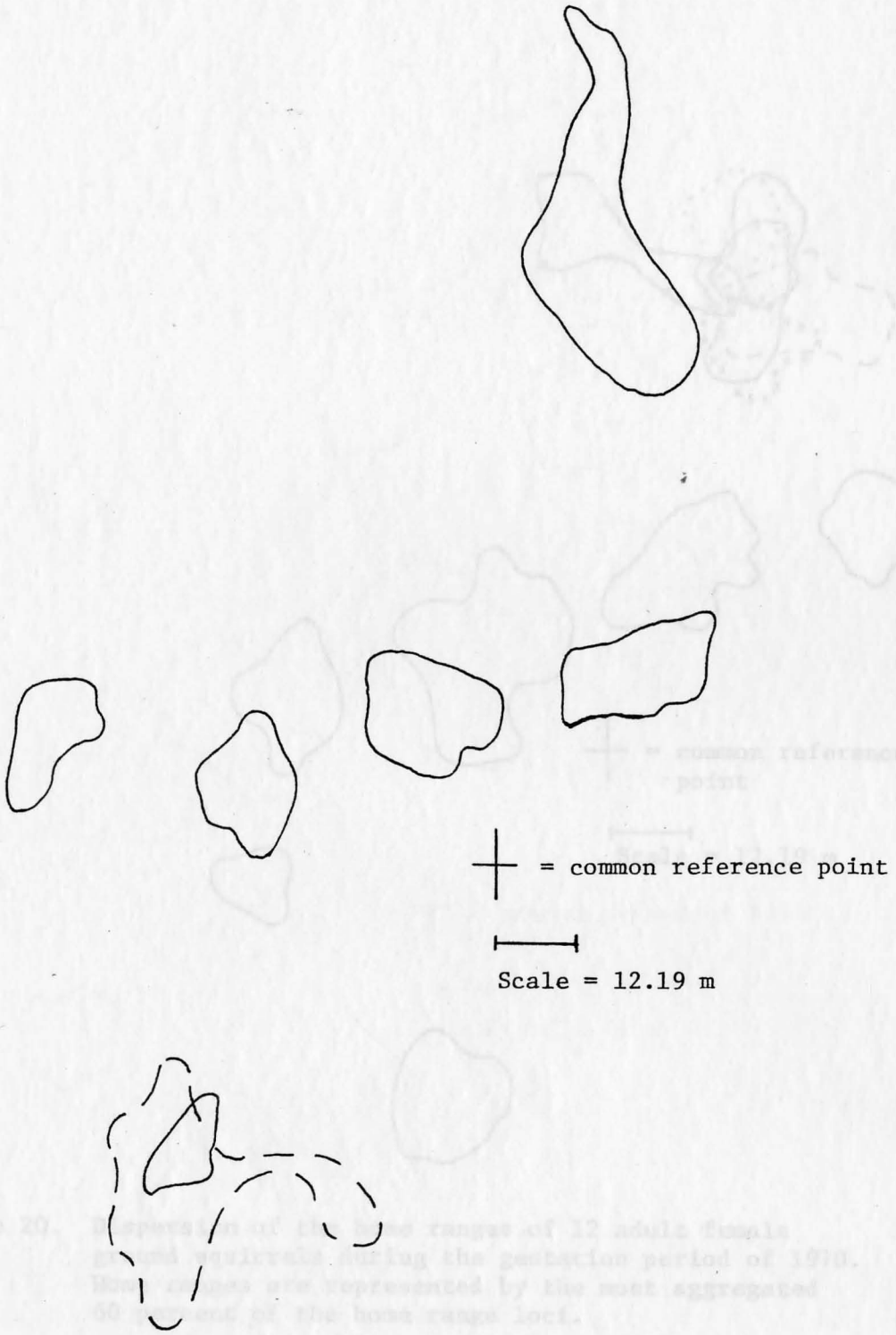

Figure 19. Dispersion of the home ranges of seven adult male ground squirrels during the fall period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

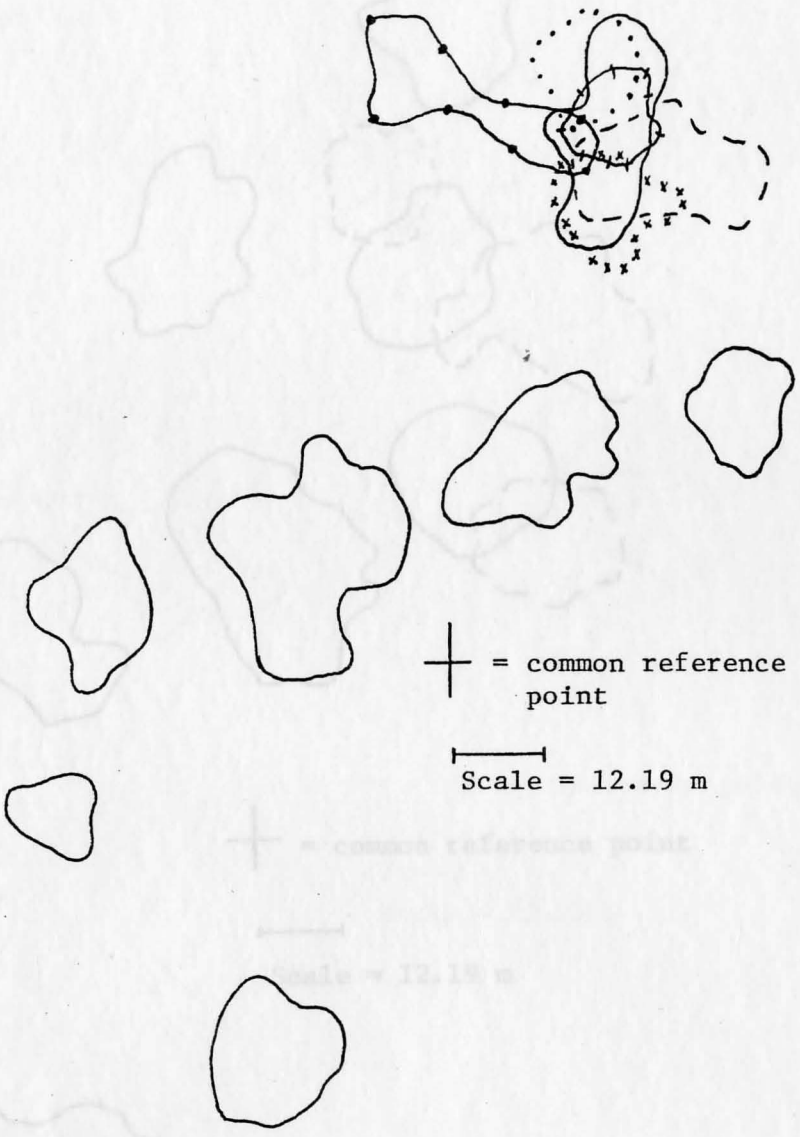

Figure 20. Dispersion of the home ranges of 12 adult female ground squirrels during the gestation period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

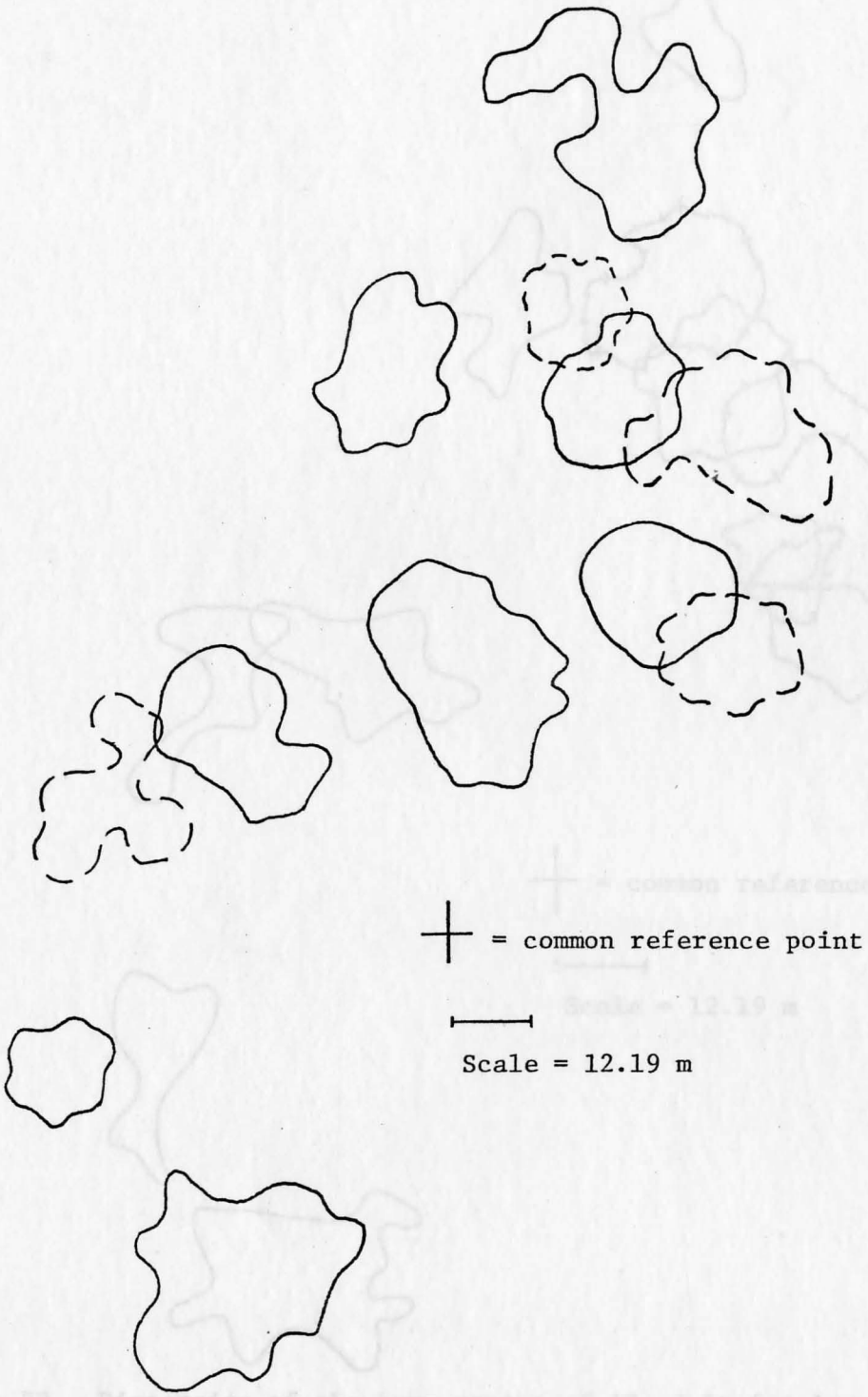

Figure 21. Dispersion of the home ranges of 12 adult female ground squirrels during the lactation period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

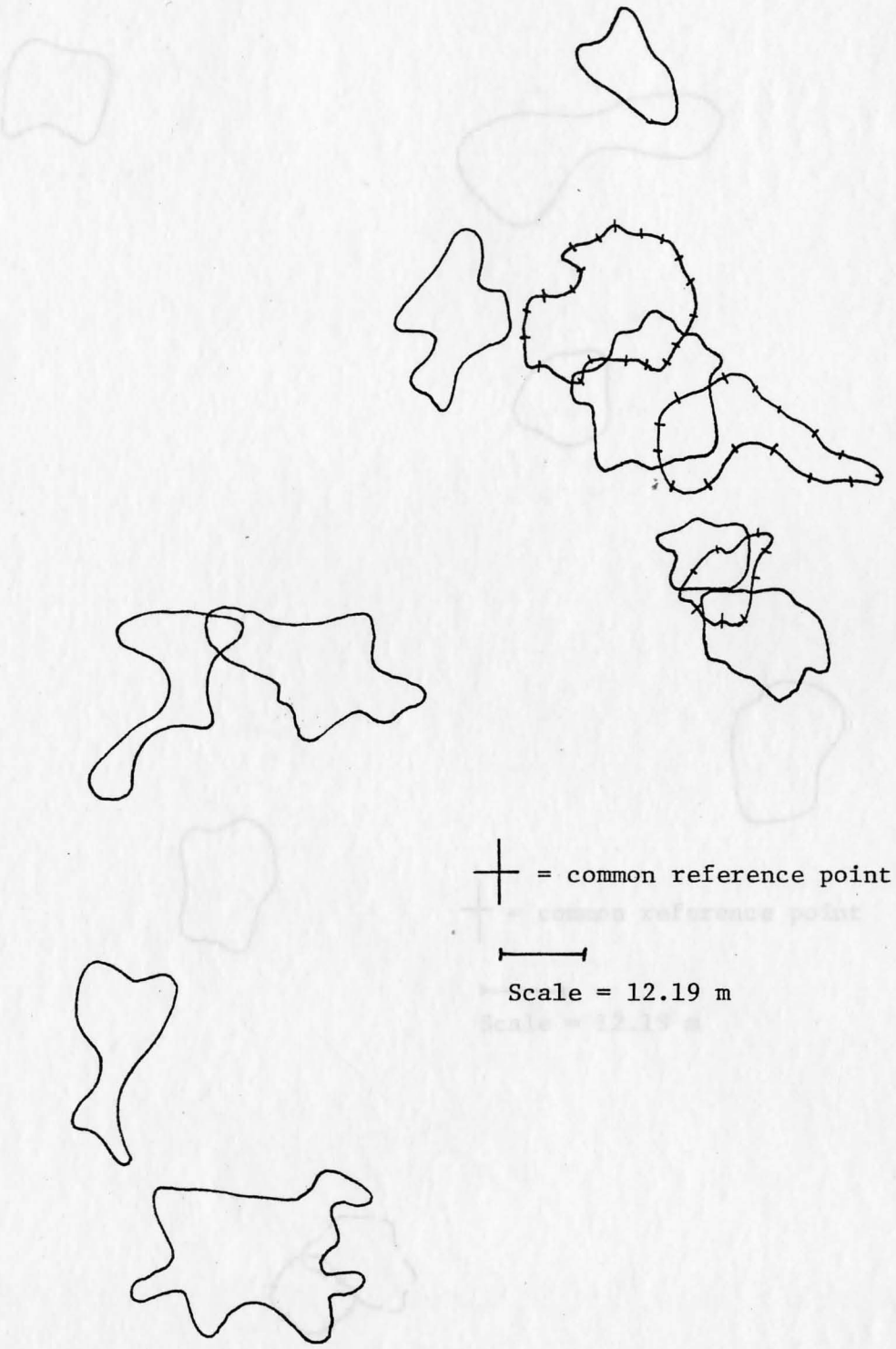

Figure 22. Dispersion of the home ranges of 12 adult female ground squirrels during the postweaning period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

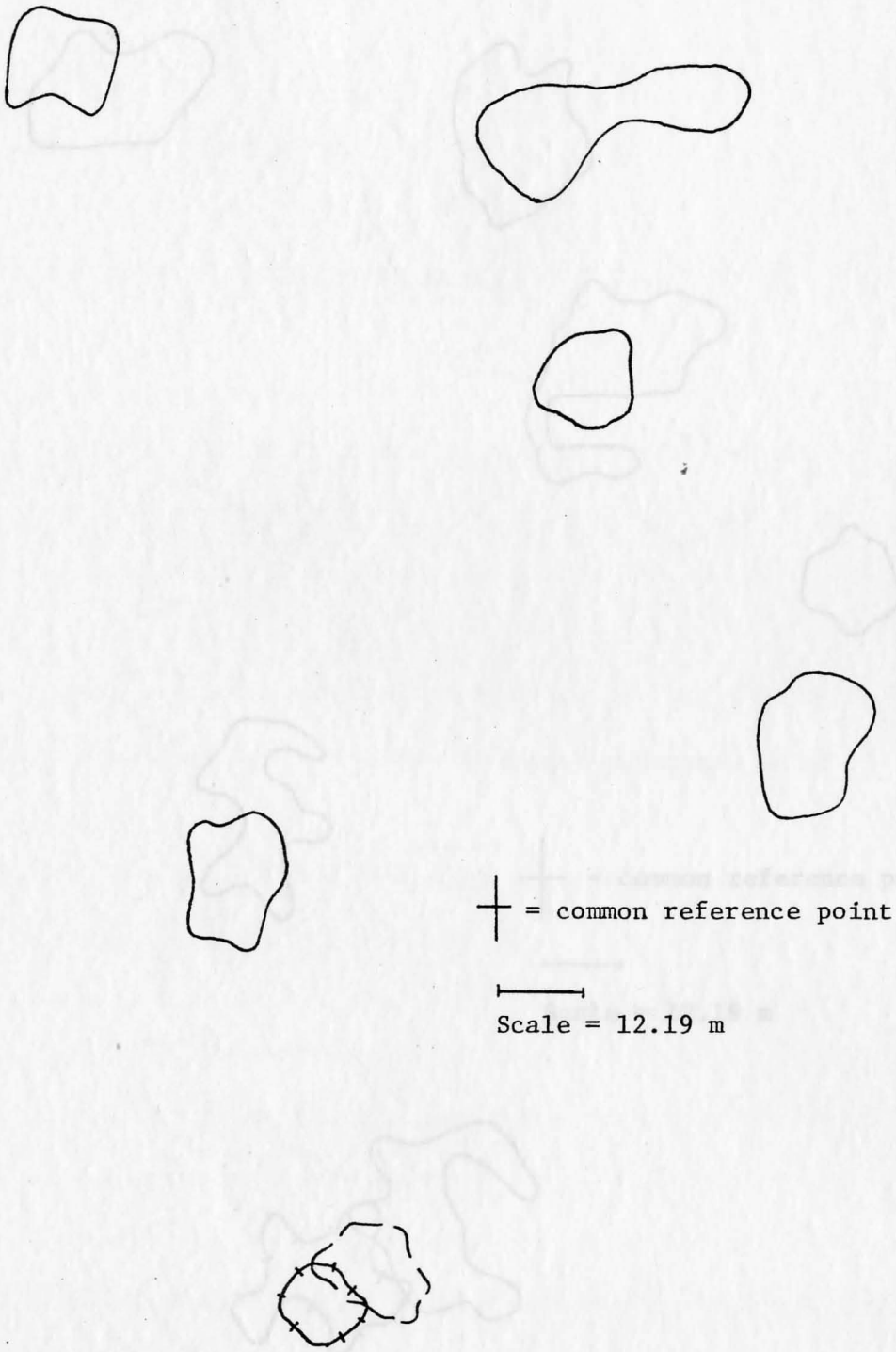

Figure 23. Dispersion of the home ranges of seven yearling females during the gestation period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

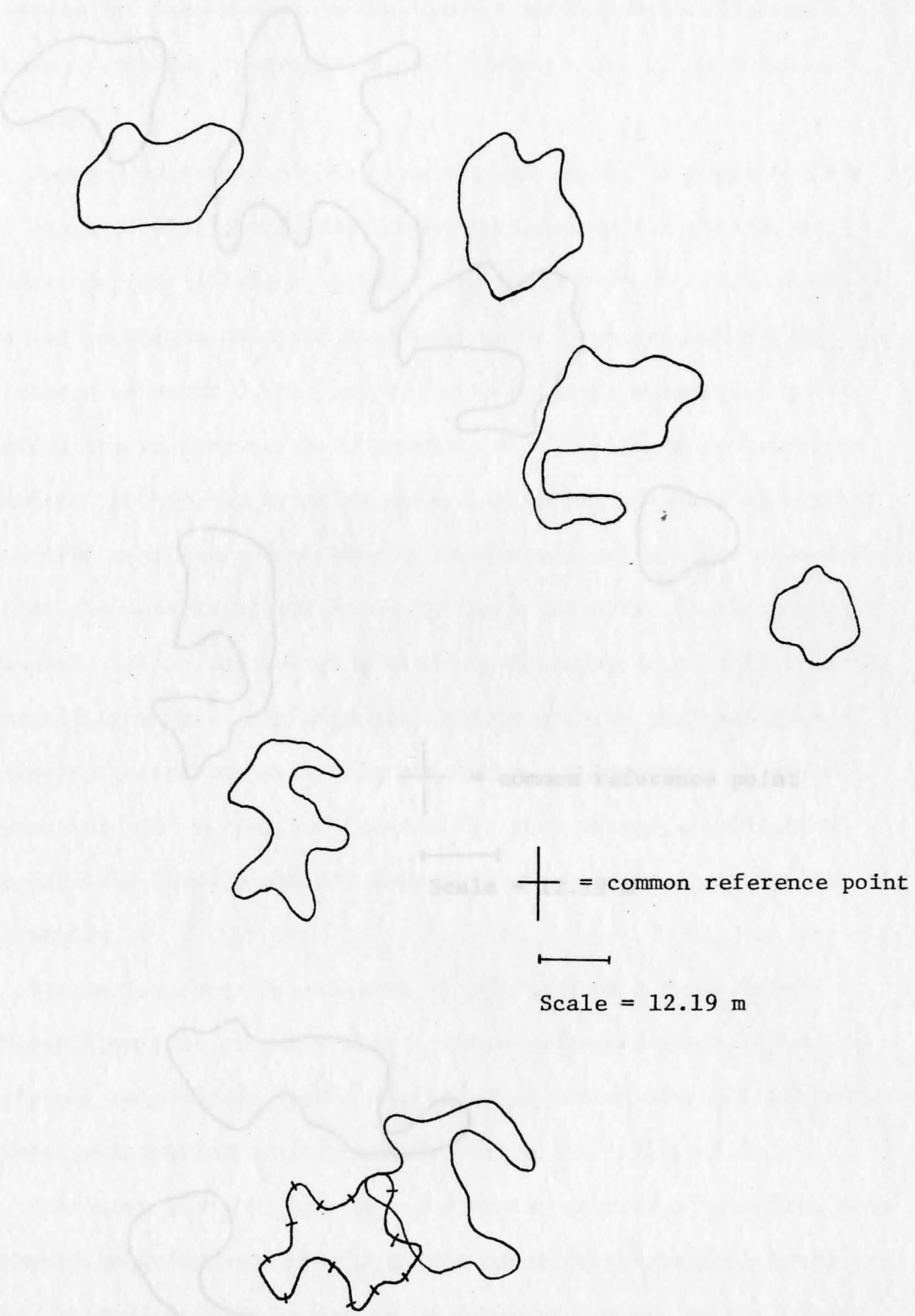

Figure 24. Dispersion of the home ranges of seven yearling females during the lactation periods of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

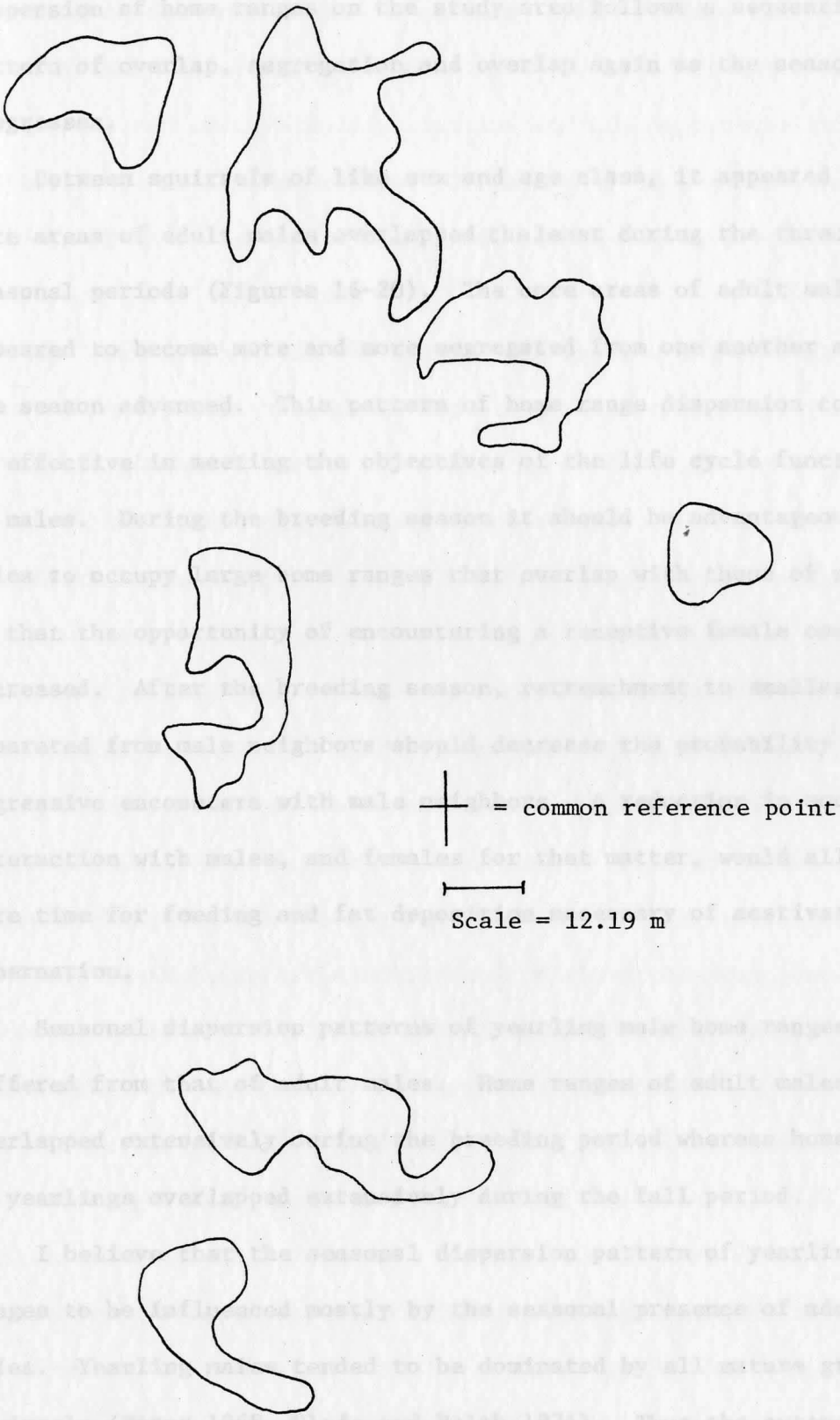

Figure 25. Dispersion of the home ranges of seven yearling females during the postweaning period of 1970. Home ranges are represented by the most aggregated 60 percent of the home range loci.

dispersion of home ranges on the study area follows a sequential pattern of overlap, segregation and overlap again as the season progresses.

Between squirrels of like sex and age class, it appeared that core areas of adult males overlapped the least during the three seasonal periods (Figures 16-20). The core areas of adult males appeared to become more and more segregated from one another as the season advanced. This pattern of home range dispersion could be effective in meeting the objectives of the life cycle functions of males. During the breeding season it should be advantageous for males to occupy large home ranges that overlap with those of neighbors so that the opportunity of encountering a receptive female could be increased. After the breeding season, retrenchment to smaller areas separated from male neighbors should decrease the probability of aggressive encounters with male neighbors. A reduction in social interaction with males, and females for that matter, would allow more time for feeding and fat deposition necessary of aestivation-hibernation.

Seasonal dispersion patterns of yearling male home ranges differed from that of adult males. Home ranges of adult males overlapped extensively during the breeding period whereas home ranges of yearlings overlapped extensively during the fall period.

I believe that the seasonal dispersion pattern of yearling home ranges to be influenced mostly by the seasonal presence of adult males. Yearling males tended to be dominated by all mature ground squirrels (Burns 1968, Slade and Balph 1974). Thus the extensive

expansion of the core areas of yearling males during their fall period (Figure 19) takes place when most of the adult males have already entered aestivation-hibernation and the aggressive levels of females is at a seasonal low. Therefore it is possible that presence of adult males and aggressive females may restrict the use of space by yearling males.

The seasonal pattern of overlap, segregation and overlap of core areas of female home ranges was associated with small home ranges during the gestation period and expanding home ranges during the lactation and postweaning periods. The extensive overlap during the gestation period is associated with emerging females' attempts to localize their use of space and with males moving about in search of receptive females. Under these conditions extensive overlap of core areas should be realized. The segregation and expansion of core areas during the lactation period is believed to result from high aggressive levels and increased energetic requirements. Females become aggressive shortly after being bred (Burns 1968, Slade and Balph 1974) and remain aggressive until shortly after the young emerge from the natal burrows. This leads to segregation of home ranges. Concurrently the metabolic requirements of a reproducing female increase during gestation to a peak during lactation. Expansion of the home range likely results from the need for more foods to meet the increased metabolic demands. Segregation of home ranges likely results from the high aggressive behavior which functions to localize the movements of neighbors. The large overlapping home ranges of postweaning females is likely the result of the lack of aggressive behavior among females and the need to secure adequate foods for

prehibernation fat deposition. The diet of ground squirrels during the last third of the season is dominated by seeds and herbs (Walker 1968). The dispersed distribution of these foods may contribute to the large home ranges of all animals during this period.

In summary, the home ranges of ground squirrels fluctuate in size and in degree of overlap with period of the season. Some of the contributing factors of this flux are sex-related life cycle functions, seasonal changes in aggressive behavior and metabolic requirements, and the availability and distribution of food resources in time and space.

Spatial distribution of behaviors within the home range

Numbers of neighbors and distribution of behaviors in the home range. A basic assumption of biologists is that the presence or absence of conspecifics influences the way in which animals use space. To determine if this were true for ground squirrels, I compared the number of neighbors of a ground squirrel against the chi-square value resulting from comparing the distribution of their behaviors within the home range with the distribution of home range loci. The chi-square values were used to indicate the degree to which the distribution of behaviors differed from the distribution of home range loci. Numbers of neighbors were defined as those individuals, male or female, whose most central 80 percent home range loci overlapped or bordered the residents' most central 80 percent of home range loci. The degree to which numbers of neighbors influenced the distribution of behaviors within the home range was

assessed by correlating these parameters for all males and all females during three periods of the year.

Among males, numbers of neighbors were significantly correlated ($P<.01$) with distribution of behaviors within the home range during their breeding and postbreeding periods but not during the fall period (Figure 26). Among females, numbers of neighbors were significantly correlated ($P<0.01$) with distribution of behaviors within the home range during the gestation and postweaning periods but not during the lactation period (Figure 27). In the cases of significant correlation, the distribution of behaviors within the home range became more and more unlike the distribution of home range loci as the numbers of neighbors increased. That is, more discretely distributed within the home range. Numbers of neighbors account for 58 and 92 percent, respectively, of the variation in the distribution of behaviors within the home ranges of breeding and postbreeding males. Numbers of neighbors account for 52 and 51 percent, respectively, of the variation in the distribution of behaviors within the home ranges of pregnant or postweaning females. Thus, it appears that numbers of neighbors are an important factor in the manner in which ground squirrels use space.

A seasonal difference in the correlation of numbers of neighbors and distribution of behaviors were observed between male and female ground squirrels. This would suggest a differential response to neighbors by sex associated with the seasonal "objectives" of each sex group. Among breeding males home ranges were large and overlapped extensively with their neighbors' home ranges. Under conditions in which trespass into adjacent home ranges is common and

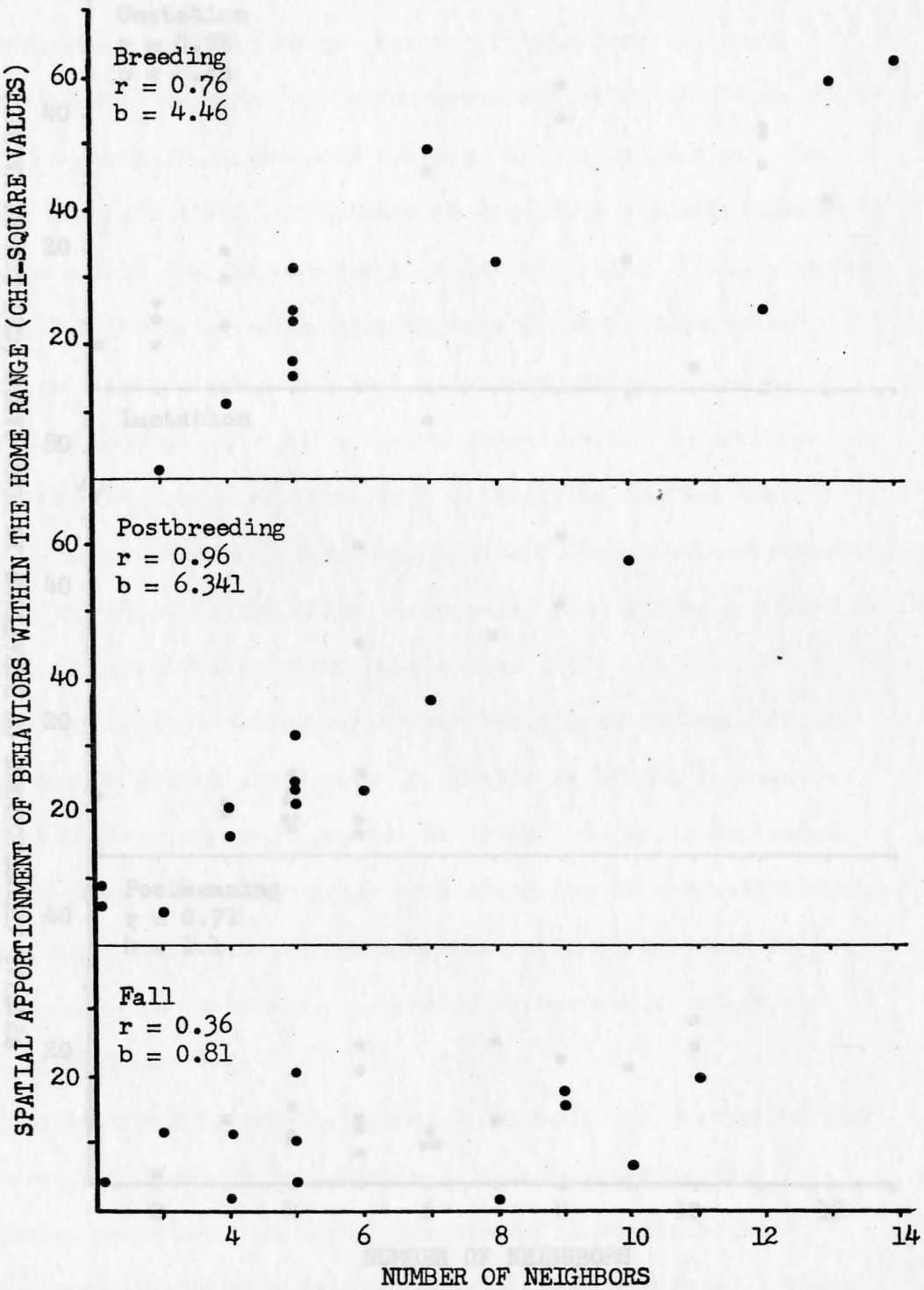

Figure 26. Relationship of number of neighbors and spatial apportionment of behaviors within the home ranges of male Uinta ground squirrels during periods of the 1970 season.

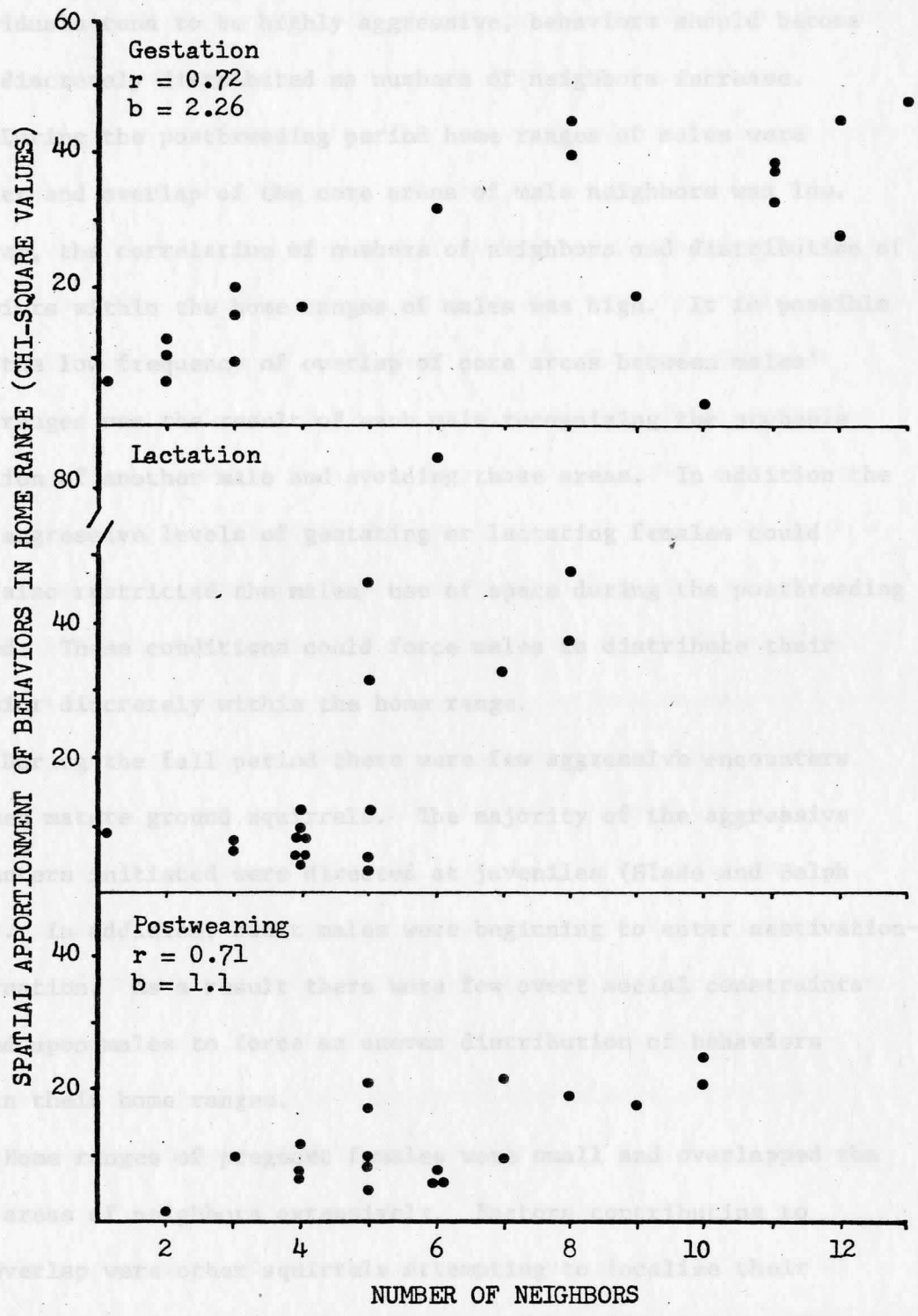

Figure 27. Relationship of number of neighbors and spatial apportionment of behaviors within the home ranges of female Uinta ground squirrels during periods of the 1970 season.

individuals tend to be highly aggressive, behaviors should become more discretely distributed as numbers of neighbors increase.

During the postbreeding period home ranges of males were smaller and overlap of the core areas of male neighbors was low. However, the correlation of numbers of neighbors and distribution of behaviors within the home ranges of males was high. It is possible that the low frequency of overlap of core areas between males' home ranges was the result of each male recognizing the probable location of another male and avoiding those areas. In addition the high aggressive levels of gestating or lactating females could have also restricted the males' use of space during the postbreeding period. These conditions could force males to distribute their behavior discretely within the home range.

During the fall period there were few aggressive encounters between mature ground squirrels. The majority of the aggressive encounters initiated were directed at juveniles (Slade and Balph 1974). In addition, adult males were beginning to enter aestivation-hibernation. As a result there were few overt social constraints placed upon males to force an uneven distribution of behaviors within their home ranges.

Home ranges of pregnant females were small and overlapped the core areas of neighbors extensively. Factors contributing to the overlap were other squirrels attempting to localize their use of space and the extensive movement of breeding males. These conditions could result in females distributing their behaviors discretely within the home range.

The relationship of spatial apportionment of behaviors within the home range of lactating females and numbers of neighbors was not continuous (Figure 27). However, two groupings of chi-square values were observed. One group of six females had chi-square values above 30.0 and a group of 12 females had chi-square values below 15.0. Five females of the group having high chi-square values emerged during D.S.E. 0-9. Additionally, all females with high chi-square values lost or gained a neighbor during their lactation periods. It is possible that the high degree of behaviors being discretely distributed within the home ranges of these females are the result of 1) attempting to expand their home ranges during a period in which other squirrels are attempting to establish their own areas of use, 2) the social adjustment to loss or gain of a new neighbor during lactation, and 3) attempting to expand the home range while males are still sexually active. Conversely, all females with low chi-square values (below 15.0) had the same neighbors as they had during the gestation period and the majority had emerged from hibernation within 10 days of one another. These animals were closely synchronized in the dates they entered lactation and it is possible that they were able to establish dominance-subordinance relationships with their neighbors during gestation.

The correlation of numbers of neighbors and distribution of behaviors among postweaning females is believed to be due to an indirect association of neighbors. The indirect factor is thought to be number of juveniles in the area, which is roughly proportional

to the number of female neighbors. In attempting to establish residence in the area, juveniles become aggressive (Balph, personal communication). It is possible that the increase in numbers of new squirrels (juveniles) attempting to establish residence within the home ranges of females would have contributed to behaviors becoming more discretely distributed as numbers of neighbors increase among postweaning females.

Spatial distribution of behaviors within the home range. I could discriminate three possible ways in which a specific behavior could be distributed within the home range using the Kruskal and Wallis' procedure. If the dispersion indices associated with a specific behavior tended to have low index values, the behavior tended to be exhibited most often in the home range areas of greatest use, hence centrally distributed. Conversely, if the dispersion indices associated with a behavior tended to be high, the behavior was classified as being peripherally distributed in the home range. If the dispersion indices of a specific behavior tended to be ranked in the same manner as the dispersion indices of the home range loci, the behavior was classified as being distributed in the same manner as the home range loci were distributed, this is, proportional to the distribution of home range loci. Because nest gathering and calling behaviors were exhibited few times by squirrels, no attempt was made to define their distributions within a home range.

So that I would be able to represent the relative characteristics of a behavior being distributed centrally, peripherally or in the same

manner as home range loci were distributed I transformed the statistics of the Kruskal and Wallis' procedure into Z statistics. Briefly, the manner in which the Kurskal and Wallis procedure determines if one sample is different from another is to divide the difference in mean ranks of the two samples by the expected variance. This procedure is an analog of the student's "t" test. Thus these statistics can be transformed into Z statistics directly. Negative Z scores represent peripheral distributions of a behavior, positive scores represent central distributions, and scores near zero represent a behavior being proportional to the distribution of home range loci.

Animals were segregated into five groups of five animals each. The groupings were five adult males of the lawn and lawn periphery, five yearling males of the lawn and lawn periphery, five yearling females of the lawn, five adult females of the lawn, and five adult females of the sage-grass and lawn periphery. The statistics used to describe distribution of behaviors within the average home range were the mean and standard deviation of the group Z scores. These statistics were used to determine 1) if there were differences in the way specific behaviors were distributed between seasonal periods and 2) if specific behaviors tended to be distributed in a different manner than home range loci were distributed.

The pooled distribution of feeding, moving, encounters, upright, motionless and grooming of 25 aimals were determined during three periods of the season (Figure 28). It is apparent from the way the standard deviations of each behavior during the three seasonal periods overlap that there were no significant

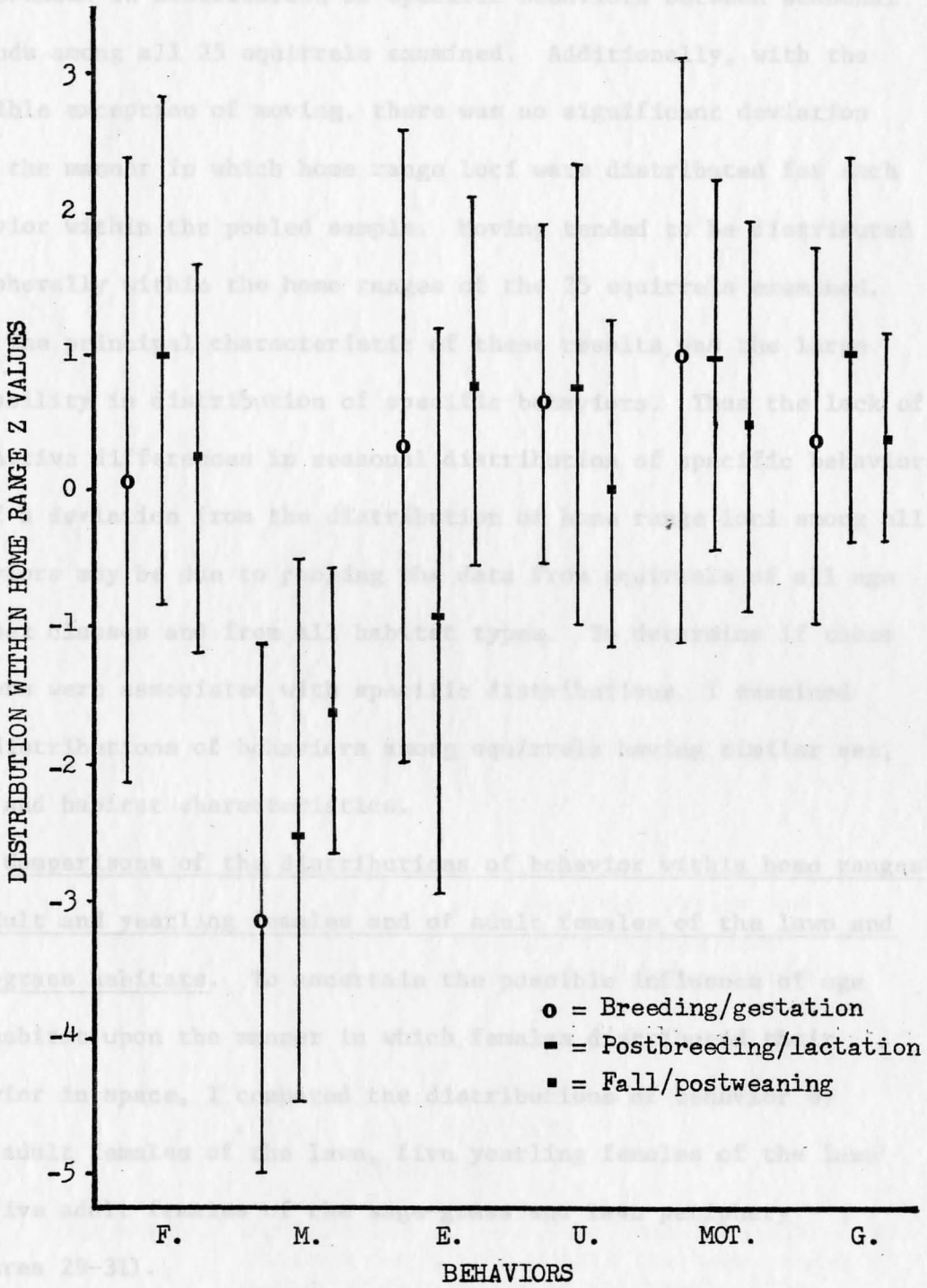

Figure 28. Distribution of behaviors (mean location $\pm$ one standard deviation) within the home ranges of 25 male and female ground squirrels (pooled data) during periods of the 1970 season.

differences in distribution of specific behaviors between seasonal periods among all 25 squirrels examined. Additionally, with the possible exception of moving, there was no significant deviation from the manner in which home range loci were distributed for each behavior within the pooled sample. Moving tended to be distributed peripherally within the home ranges of the 25 squirrels examined.

The principal characteristic of these results was the large variability in distribution of specific behaviors. Thus the lack of definitive differences in seasonal distribution of specific behaviors or of a deviation from the distribution of home range loci among all behaviors may be due to pooling the data from squirrels of all age and sex classes and from all habitat types. To determine if these factors were associated with specific distributions, I examined the distributions of behaviors among squirrels having similar sex, age, and habitat characteristics.

Comparisons of the distributions of behavior within home ranges of adult and yearling females and of adult females of the lawn and sage-grass habitats. To ascertain the possible influence of age and habitat upon the manner in which females distributed their behavior in space, I compared the distributions of behavior by five adult females of the lawn, five yearling females of the lawn and five adult females of the sage-grass and lawn periphery (Figures 29-31).

There were three main conclusions that can be made of the manner in which behaviors were distributed within the home ranges of these three groups of females. The first conclusion was that due to the

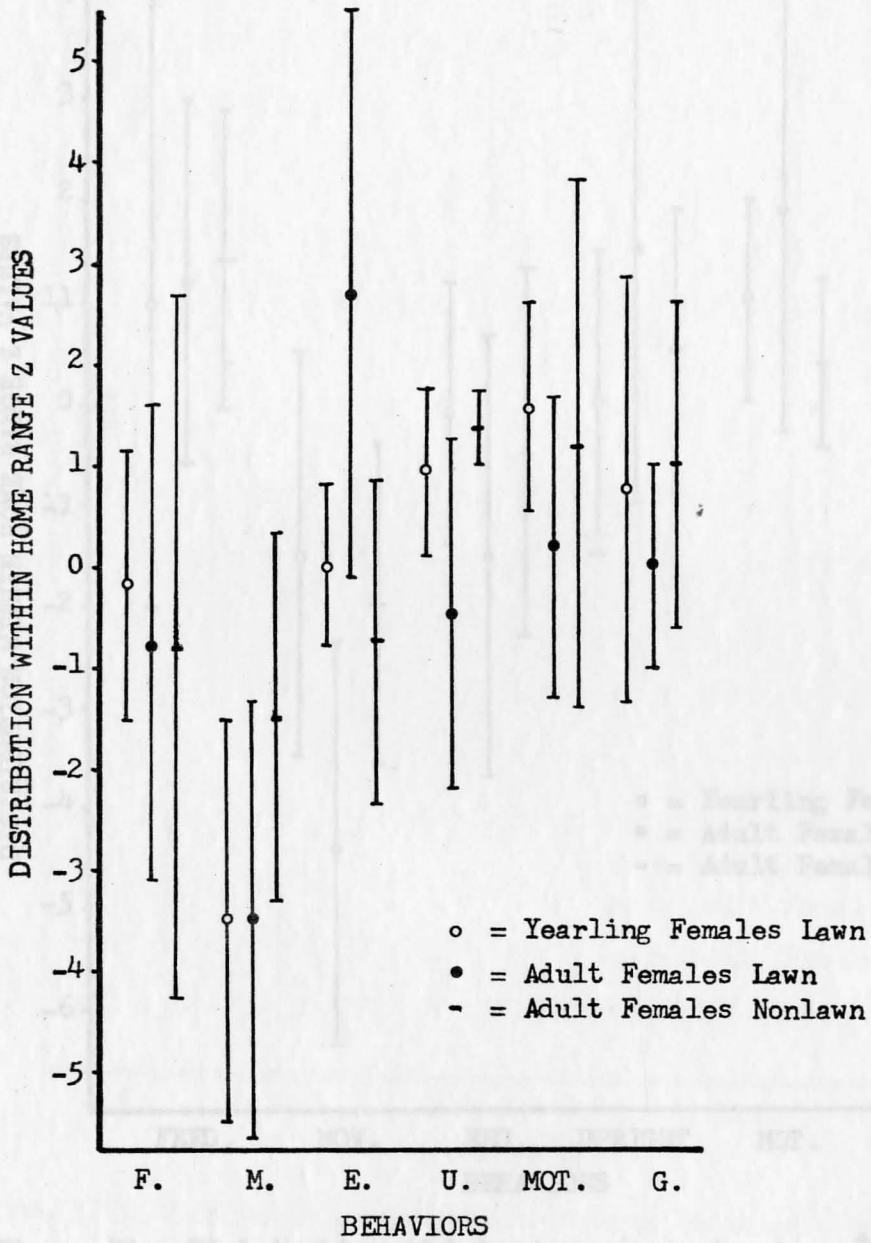

Figure 29. Distribution of behaviors (mean location ± one standard deviation) within the home ranges of gestating female ground squirrels, 1970.

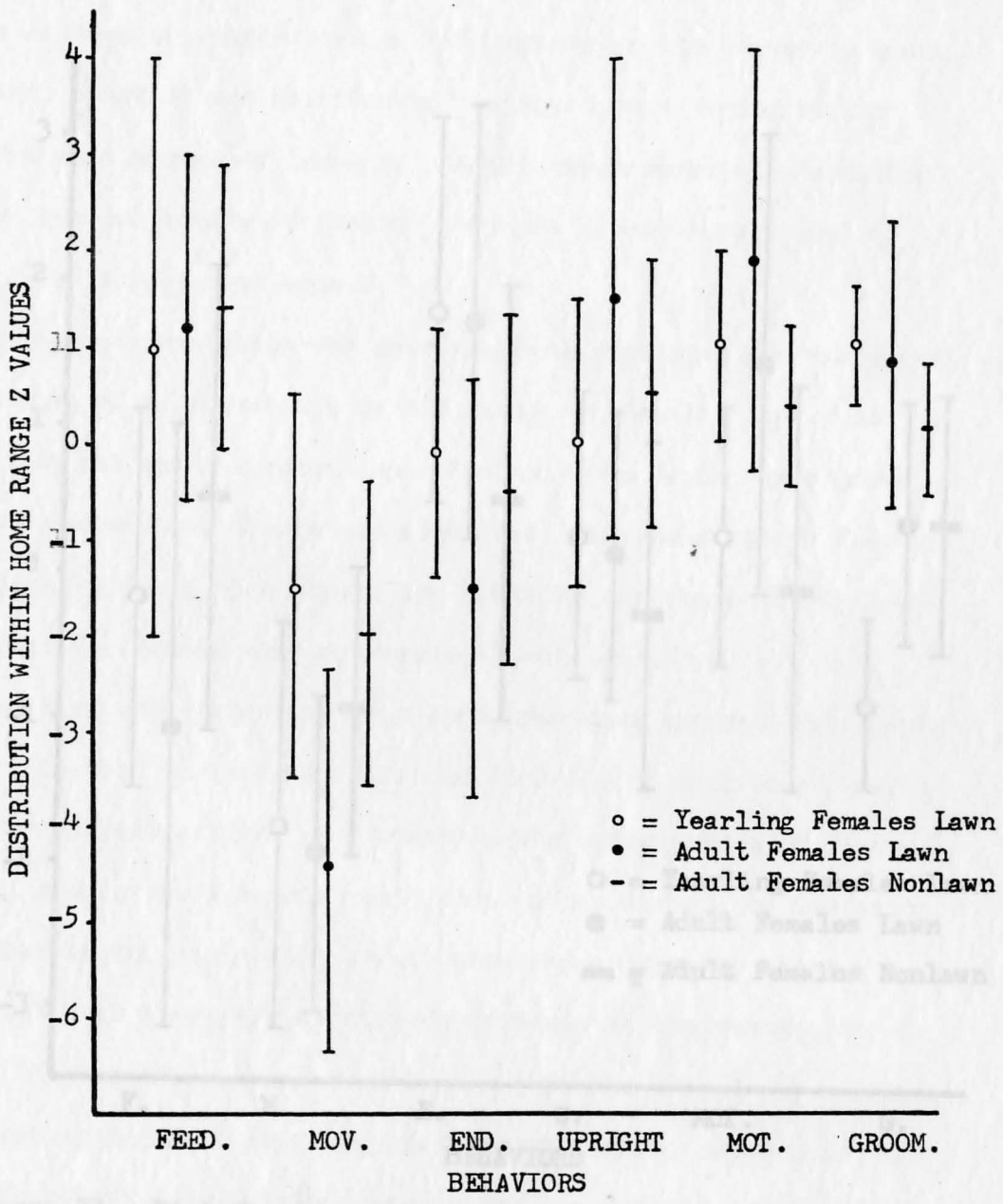

Figure 30. Distribution of behaviors (mean location ± one standard deviation) within the home ranges of lactating female ground squirrels, 1970.

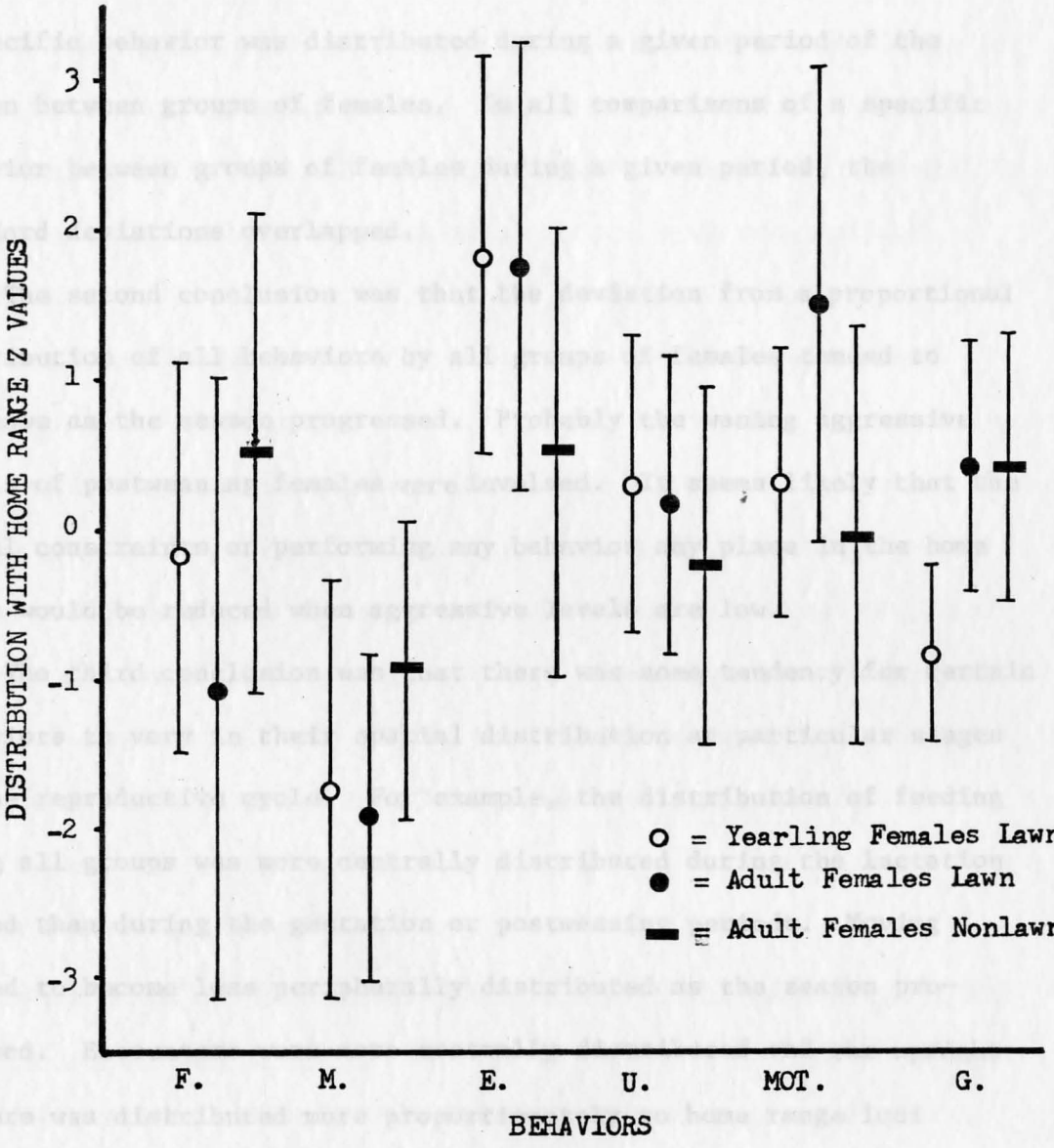

Figure 31. Distribution of behaviors (mean location ± one standard deviation) within the home ranges of postweaning female ground squirrels, 1970.

variation in distribution of specific behaviors among members of a group of females, there were no differences in the manner in which a specific behavior was distributed during a given period of the season between groups of females. In all comparisons of a specific behavior between groups of females during a given period, the standard deviations overlapped.

The second conclusion was that the deviation from a proportional distribution of all behaviors by all groups of females tended to decrease as the season progressed. Probably the waning aggressive levels of postweaning females were involved. It seems likely that the social constraints on performing any behavior any place in the home range would be reduced when aggressive levels are low.

The third conclusion was that there was some tendency for certain behaviors to vary in their spatial distribution at particular stages of the reproductive cycle. For example, the distribution of feeding among all groups was more centrally distributed during the lactation period than during the gestation or postweaning periods. Moving tended to become less peripherally distributed as the season progressed. Encounters were more centrally distributed and the upright posture was distributed more proportionately to home range loci during the postbreeding period than during the gestation or lactation periods.

The more central distribution of feeding during the lactation period by all females may be the result of the expansion of the home range and segregation of the core areas between females. Since the energy requirements of lactation are approximately double those of nonreproducing females (Kleiber 1961), feeding in the core areas

could be advantageous in that the high energetic demands are met in areas of little disturbance from neighbors.

The decrease in the peripheral distribution of moving during the lactation and postweaning periods is likely an artifact of expanding home range size. As size of the home range increases the probability of observing an animal moving anywhere in its home range should increase.

The central distribution of encounters and the proportional distribution of the upright posture during postweaning are associated with the low aggressive levels and seasonal maximum in home range size during this period. With increased tolerance of conspecifics, encounters become most probable in those areas of greatest use, the central regions of the home range. With fewer aggressive encounters between conspecifics it is likely that upright behavior is largely a response to predators. In a large home range it would be advantageous for predator response (upright) to be proportional to the home range use pattern.

Comparisons of the distributions of behavior within home ranges of adult and yearling males. The manner in which five adult males and five yearling males distributed their behavior in space during three periods of the season were compared (Figures 32-34).

Like females, variation in the distribution of specific behaviors among yearling males and adult males was large. Due to the overlap of the standard deviations of each behavior each period of the season it was concluded that no differences in distribution of specific bheaviors between the two groups existed.

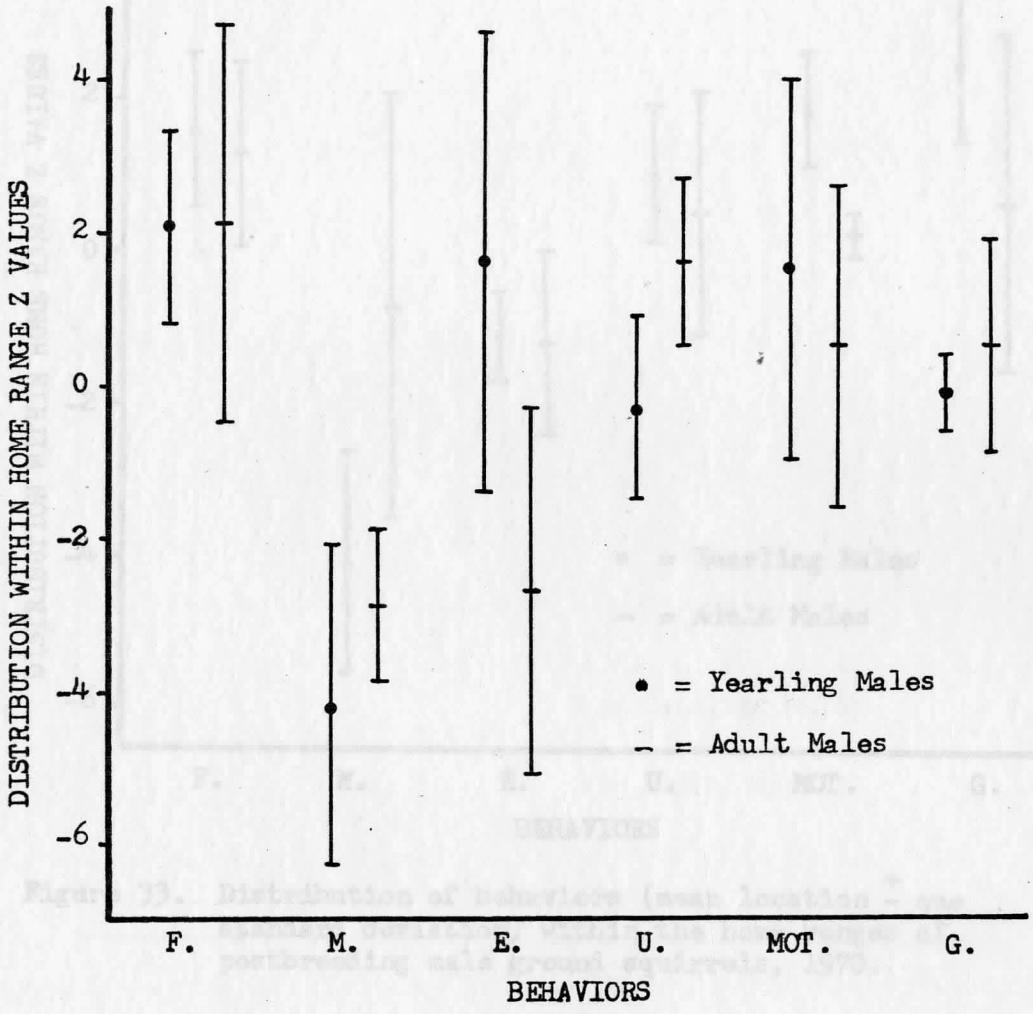

Figure 32. Distribution of behaviors (mean location ± one standard deviation) within the home ranges of breeding male ground squirrels, 1970.

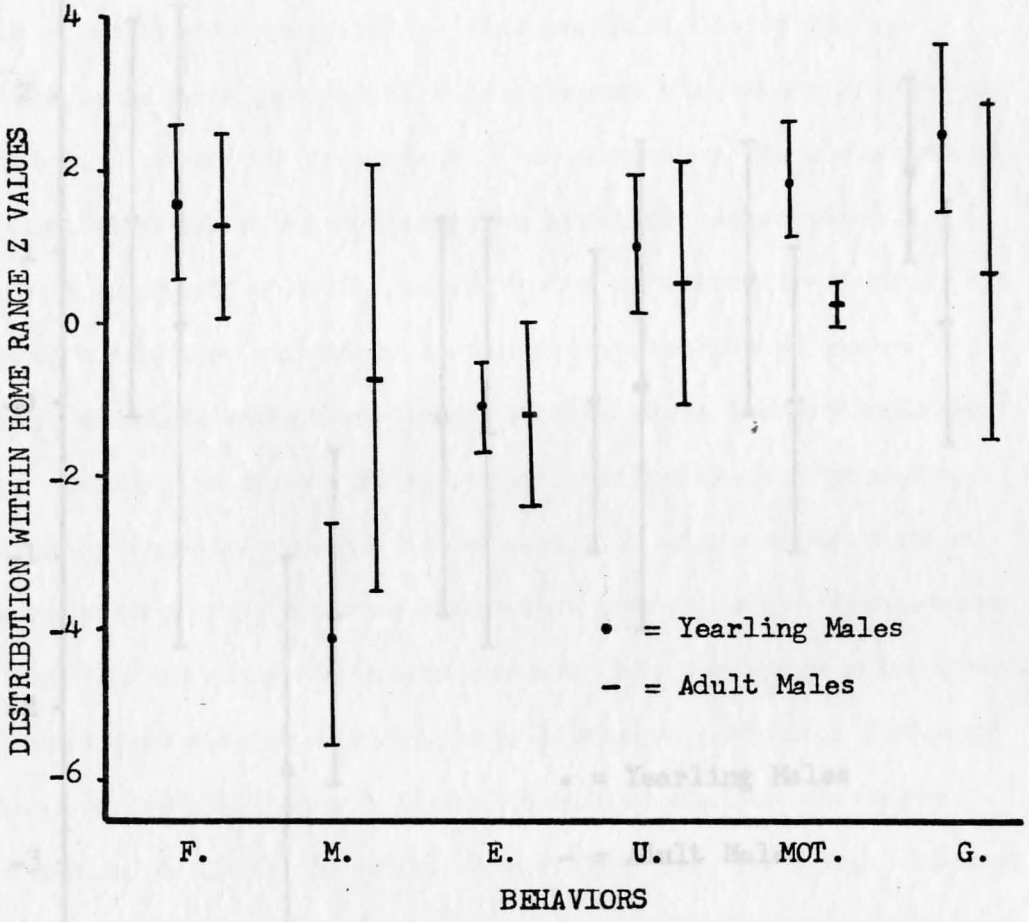

Figure 33. Distribution of behaviors (mean location $\pm$ one standard deviation) within the home ranges of postbreeding male ground squirrels, 1970.

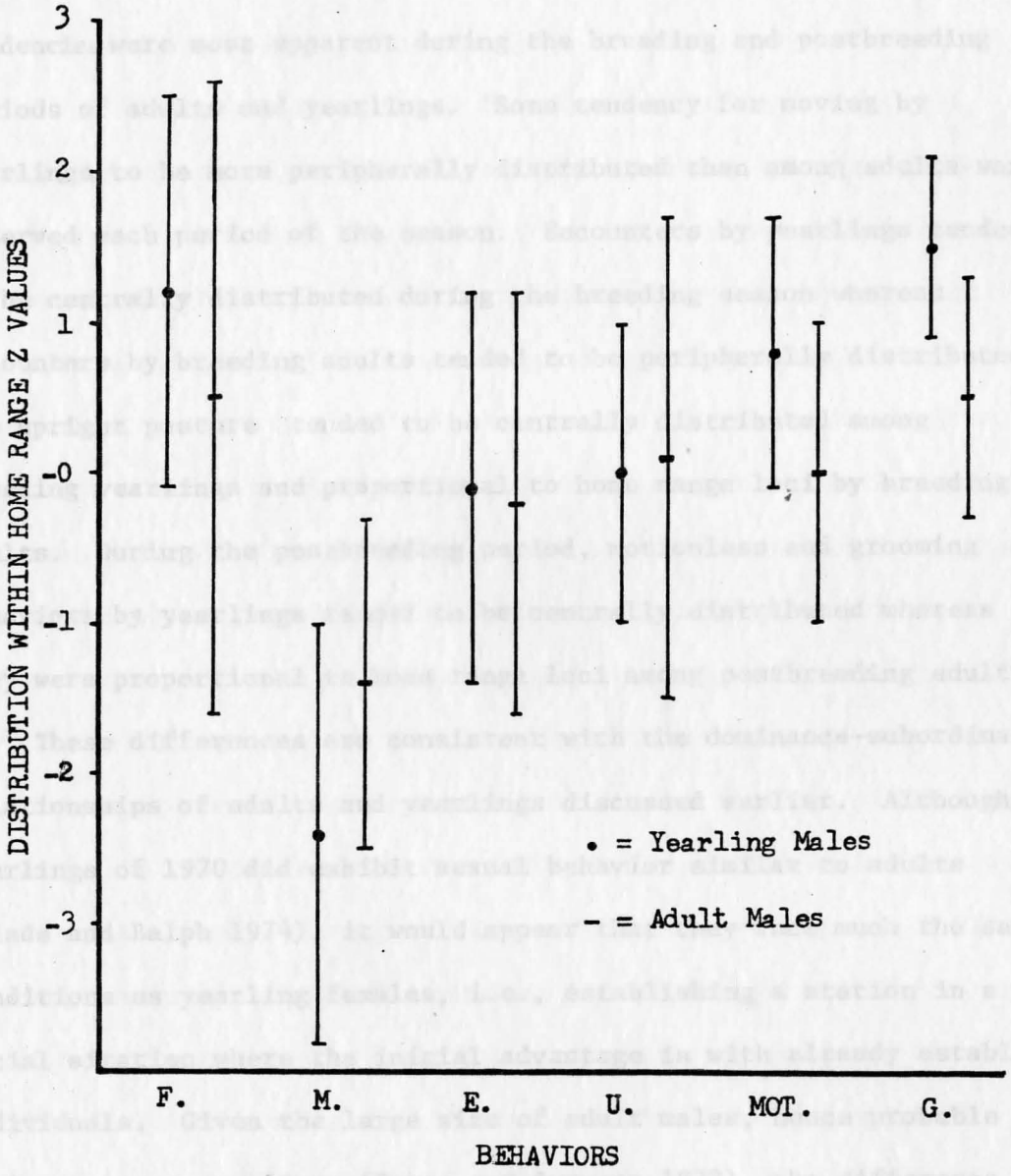

Figure 34. Distribution of behaviors (mean location ± one standard deviation) within the home ranges of male ground squirrels during the fall period, 1970.

Some tendencies for difference in distribution of specific behaviors between adults and yearlings were however, noted. These tendencies were most apparent during the breeding and postbreeding periods of adults and yearlings. Some tendency for moving by yearlings to be more peripherally distributed than among adults was observed each period of the season. Encounters by yearlings tended to be centrally distributed during the breeding season whereas encounters by breeding adults tended to be peripherally distributed. The upright posture tended to be centrally distributed among breeding yearlings and proportional to home range loci by breeding adults. During the postbreeding period, motionless and grooming behaviors by yearlings tended to be centrally distributed whereas they were proportional to home range loci among postbreeding adults.

These differences are consistent with the dominance-subordinance relationships of adults and yearlings discussed earlier. Although yearlings of 1970 did exhibit sexual behavior similar to adults (Slade and Balph 1974), it would appear that they face much the same conditions as yearling females, i.e., establishing a station in a social sitation where the initial advantage is with already established individuals. Given the large size of adult males, hence probable dominance over yearlings (Payne and Swanson 1972), the difference in testosterone metabolism (Ellis and Balph 1976) and the late emergence of yearlings (most yearlings emerged after D.S.E. 19) it is surprising that the two groups did not differ more in the spatial distribution of their behaviors.

Differences in the spatial distribution of behaviors of males and females. The distribution of behaviors among males differed from that

among females. The differences were principally in the distributions of feeding and encounters during breeding/gestation and during the fall/postweaning periods (Figures 29-34). Feeding by males occurred centrally throughout all periods but females fed centrally only during lactation. The distribution of encounters by males tended to be peripheral during the breeding period, whereas encounters by females tended to be peripheral only during the lactation period.

In conclusion, it appears that each specific behavior was distributed in more or less the same way by all groups of squirrels. This lack of difference in distribution of specific behaviors within the home range between groups of squirrels is due to the large degree of individual variation in distribution of behaviors within each group. This individual variation would suggest that each squirrel is particularly responsive to the unique distribution of environmental conditions and social conditions within its home range. This interpretation is consistent with the results of correlating numbers of neighbors with spatial apportionment of behaviors (Figures 26-31). In that analysis, behaviors tended to become more discretely distributed as numbers of neighbors increased. Therefore, I have concluded that while the distribution of behaviors by groups of squirrels was similar each period of the season, each individual probably distributes its behavior differently from other squirrels. This conclusion would be consistent with the variation in numbers of neighbors and environmental characteristics of each home range.

Spatial distribution of aggressive encounter components

Introduction. If a function of aggression is to regulate the use of space, then it is important to examine the spatial distribution of the various components of aggressive encounters. Parameters of interest are the distributions of distances between individuals at encounter initiation, spatial distribution of encounters initiated by and upon the home range resident, and the spatial distribution of encounter wins, draws and losses.

Distances between individuals at the initiation of an encounter. Distances between individuals at the initiation of an aggressive encounter during periods of the 1970 season were determined (Table 22). These data represent all the aggressive encounters initiated by the squirrels used for spatial analysis of behavior. Thus, some encounters were initiated upon individuals other than those selected for spatial analysis of behavior.

Differences were observed in the frequency squirrels initiated encounters with individuals of the same sex and in the distance between individuals at the initiation of an encounter. Females initiated 55 percent of 985 encounters with males and 45 percent with other females. In contrast males initiated many more encounters with other males (75 percent of 476) than they did with females. When females initiated encounters with males, 50 percent of the encounters occurred at 1.5 m (5 ft) or less whereas 63 percent of the encounters with other females occurred at this distance. Forty-five percent of the encounters between males occurred at 1.5 m or less whereas 67 percent of the encounters initiated by males with

Table 22. Percent frequency of the distance between individuals at the initiation of agonistic encounters for adult and yearling male and female Uinta ground squirrels during phases of the 1970 season at the Utah State University Forestry Field Station, Cache National Forest, Utah.

Participants in Encounters	Time of Season	Distance Interval Between Individuals*									
		N	1	2	3	4	5	6	7	8	9
Adult Females	A	178	69	16	8	4	0.6	0.6	0.6		
Initiating On	B	110	49	16	18	5	4	3	3	1	1
Females	C	49	90	2	6	1					
Adult Females	A	247	45	26	15	9	2	2	0.4	0.4	1
Initiating On	B	132	33	23	23	8	7	0.8	3	0.8	3
Males	C	45	80	13	7						
Yearling Females	A	47	51	23	17	6	2				
Initiating On	B	33	52	30	9	3	3	3			
Females	C	24	83	13	4						
Yearling Females	A	50	70	12	10	6	2				
Initiating On	B	42	67	10	12	5	2		2		2
Males	C	28	68	18	11		4				
Adult Males	D	73	41	30	16	7	1	1			3
Initiating On	E	11	45	36	9		9				
Males	F	25	76	12	8		4				
Adult Males	D	18	83	17							
Initiating On	E	1	100								
Females	F	9	100								
Yearling Males	D	177	40	34	10	7	3	3	1	1	0.6
Initiating On	E	51	41	29	8	10	2	6		4	
Males	F	37	68	24	8						
Yearling Males	D	33	61	15	15	6		3			
Initiating On	E	29	48	24	14	7	3	3			
Females	F	32	72	6	6	9	3	3			

A = Gestation
B = Lactation
C = Postweaning
D = Breeding
E = Postbreeding
F = Fall

*Distance interval in increments of 1.5 m (5 ft.), 1 = 0-1.5 m, 2 = 1.5-3 m and 9 = greater than 12.0 m.

females occurred at this distance. Because of these differences and the intensity of sexual activity by males in 1970 (males were more sexually active during 1970 than in any other year, Slade and Balph 1974), I attribute the disproportionate aggession by females toward males as repulsing of sexual advances. The high frequency (relative to adults) of encounters initiated by yearling males with females is associated with their home ranges being located within a concentration of females (see Figures 16-25).

Three conclusions can be drawn from these data. The first conclusion is that the majority of aggressive encounters between squirrels occur when the animals are in close proximity. The second conclusion is that there is seasonal variability in intensity of aggression (measured here by distance between squirrels at the initiation of an encounter). This intensity being lowest during the last period of the season. The third conclusion is that if we are able to discount the disproportionate aggression of females with males as repulsing sexual advances, it would appear that the most serious competitor of a squirrel is an individual of the same sex. Because of the differential number of encounters males had with other males relative to females and the intensity of sexual activity of males during 1970, the following examinations of distributions of aggressive encounters and their results within the home range will deal only with encounters between squirrels of like sex.

Spatial distribution of encounters initiated by and upon home range residents. Spatial distributions of encounters between

squirrels of like sex within five regions of the home ranges of squirrels of the same sex and age class were determined (Tables 23-26). Parameters used to describe spatial distributions of encounters were 1) number of all encounters between squirrels of like sex in each region, 2) encounter rate per region (number of encounters per region ÷ number of home range loci per region), 3) the number of encounters initiated by and upon a home range resident per region, and 4) the relative percentage of total encounters in each region that were either initiated by or upon the home range resident. Each home range was divided into five regions with each region containing 20 percent of the home range loci. Thus there were equal amounts of time spent in each region. Use per unit area (number of home range loci per region ÷ number of 1.22^2 m cells occupied in each region) for each region was also determined (Table 27).

As regions of the home ranges were determined as percent of the total observations, the distributions of encounters per region of different home ranges were directly comparable. Therefore the encounters between squirrels of like sex within the same home range regions of a group of like squirrels were summed to give a composite estimate of the spatial distribution of encounters for a given group.

The spatial distribution of all encounters of home range residents varied with age of the squirrel (Tables 23-26). Within the home ranges of adults the number and rate of encounters per region were more or less constant throughout regions of the home ranges during

Table 23. Aggressive encounters between male Uinta ground squirrels in regions of the home ranges of seven adult males during periods of the 1970 season.

Seasonal Period	# Obs. Per Region	Data Type	Home Range Regions 5 #/Rate	%	4 #/Rate	%	3 #/Rate	%	2 #/Rate	%	1 #/Rate	%
Breeding	258.4	A	23		22		27		34		25	
		B	.09		.09		.10		.13		.10	
		C	11	48	12	55	14	52	14	41	6	24
		D	12	52	10	45	13	48	20	59	19	76
Postbreeding	383.8	A	4		16		6		16		19	
		B	.01		.04		.02		.04		.05	
		C	3	75	11	69	5	83	9	56	4	21
		D	1	25	5	31	1	17	7	44	15	79

A = All encounters between males in a region.
B = Total encounter rate/region (A ÷ # observations/region).
C = Encounters initiated by home range residents upon other males (number and % of total encounters/region).
D = Encounters initiated upon home range residents by other males (number and % of total encounters/region).
* = Refers to the time interval after breeding to end of the season.

Table 24. Aggressive encounters between male Uinta ground squirrels in regions of the home ranges of five yearling males during periods of the 1970 season.

Seasonal Period	# Obs. Per Region	Data Type	Home Range Regions 5 #/Rate	5 %	4 #/Rate	4 %	3 #/Rate	3 %	2 #/Rate	2 %	1 #/Rate	1 %
Breeding	312.8	A	70		65		52		39		30	
		B	.22		.21		.17		.12		.10	
		C	46	66	50	77	17	33	19	49	10	33
		D	24	34	15	23	35	67	20	51	20	67
Postbreeding	308.8	A	24		18		43		44		32	
		B	.08		.06		.14		.14		.10	34
		C	22	92	12	67	19	44	11	25	11	66
		D	2	8	6	33	24	56	33	75	21	
Fall	218.0	A	7		3		4		12		14	
		B	.03		.01		.02		.06		.06	
		C	5	71	2	67	2	50	5	42	3	21
		D	2	29	1	33	2	50	7	58	11	79

A = All encounters between males in a region.
B = Total encounter rate/region (A ÷ # observations/region).
C = Encounters initiated by home range residents upon other males (number and % of total encounters/region).
D = Encounters initiated upon home range residents by other males (number and % of total encounters/region).

Table 25. Aggressive encounters between female Uinta ground squirrels in regions of the home ranges of 12 adult females during periods of the 1970 season.

Seasonal Period	# Obs. Per Region	Data Type	Home Range Regions 5 #/Rate	5 %	4 #/Rate	4 %	3 #/Rate	3 %	2 #/Rate	2 %	1 #/Rate	1 %
Gestation	519.6	A	84		71		55		62		63	
		B	.16		.14		.11		.12		.12	
		C	66	79	43	61	32	58	33	53	13	21
		D	18	21	28	39	23	42	29	47	50	79
Lactation	624.0	A	35		46		62		36		70	
		B	.06		.07		.10		.06		.11	
		C	30	86	32	70	37	60	16	44	9	13
		D	5	14	14	30	25	40	20	56	61	87
Postweaning	260.2	A	5		6		7		11		7	
		B	.02		.02		.03		.04		.03	
		C	4	80	3	50		43	5	45	2	29
		D	1	20	3	50	4	57	6	55	5	71

A = All encounters between females in a region.
B = Total encounter rate/region (A ÷ # observations/region).
C = Encounters initiated by home range residents upon other females (number and % of total encounters/region).
D = Encounters initiated upon home range residents by other females (number and % of total encounters/region).

Table 26. Aggressive encounters between female Uinta ground squirrels in regions of the home ranges of seven yearling females during periods of the 1970 season.

Seasonal Period	# Obs. Per Region	Data Type	Home Range Regions 5 #/Rate	%	4 #/Rate	%	3 #/Rate	%	2 #/Rate	%	1 #/Rate	%
Gestation	287.8	A	7		18		30		29		28	
		B	.02		.06		.10		.10		.10	
		C	5	71	13	72	10	33	10	34	1	4
		D	2	29	5	28	20	67	19	66	27	96
Lactation	222.2	A	7		12		19		15		9	
		B	.03		.05		.09		.07		.04	
		C	6	86	8	67	8	42	4	27	2	22
		D	1	14	4	33	11	58	11	73	7	78
Postweaning	184.8	A	4		2		3		4		0	
		B	.02		.01		.02		.02		0	
		C	4	100	2	100	2	67	1	25	0	
		D	0		0		1	33	3	75	0	

A = All encounters between females in a region.
B = Total encounter rate/region (A ÷ # observations/region).
C = Encounters initiated by home range residents upon other females (number and % of total encounters/region).
D = Encounters initiated upon home range residents by other females (number and % of total encounters/region).

Table 27. Number of observations and average number of observations per 1.22^2 m cell occupied by Uinta ground squirrels per region for the composite home ranges of 7 adult males, 5 yearling males, 12 adult females and 7 yearling females during periods of the 1970 season.

Sex and Age Class	Seasonal Period	# Obs. Per Region	Average # obs. per 1.22 m^2 cell per region of home range				
			5*	4	3	2	1
Adult Males	Breeding	258.4	2.39	1.94	1.66	1.28	1.11
	Postbreeding**	383.8	2.27	1.93	1.62	1.37	1.15
Yearling Males	Breeding	312.8	4.06	3.40	2.06	1.56	1.26
	Postbreeding	308.8	3.77	3.26	2.16	1.66	1.54
	Fall	218.0	2.25	1.85	1.49	1.25	1.12
Adult Females	Gestation	519.6	4.56	3.07	2.40	1.90	1.31
	Lactation	624.0	3.74	2.49	2.10	1.67	1.18
	Postweaning	260.2	2.50	2.25	1.80	1.46	1.16
Yearling Females	Gestation	287.8	4.96	3.47	2.55	1.63	1.18
	Lactation	222.2	2.81	2.89	1.67	1.34	1.19
	Postweaning	184.8	2.32	2.32	1.73	1.36	1.16

* = Regions of the composite home ranges.
** = Refers to the time interval of after breeding to end of the season.

all periods of the year. Thus it would appear that the distribution of all encounters among adults was related to time spent in each region and independent of use per unit area of each region.

Within the home ranges of yearling ground squirrels the distribution of all encounters varied with sex and period of the season. Among yearling males during the breeding period, the number and rate of encounters decreased as distance from region five increased. The distribution appeared to be related more to use per unit area than to time spent in each region. During the postbreeding season, the number and rate of encounters were highest in regions two and three and were independent of time spent in a region or the use per unit area of each region. During the fall period there appeared to be little difference in the number or rate of encounters between regions, hence, more or less related to time spent in each region.

The number and rate of encounters per region within the home ranges of yearling females during the gestation period was highest in regions one through three. During the lactation period these parameters peaked in the midregion of the home ranges, and during the postweaning period there appeared to be no regional difference in the distribution of all encounters between females. Thus it would appear that the distribution of number and rate of encounters within the home ranges of yearling females was independent of time spent in regions or use per unit area of each region during the gestation and lactation periods and related to time spent in regions of the home range during the postweaning period.

In contrast to the variation observed in the distributions of all encounters among groups of squirrels, the distributions of the

percentage of all encounters that were initiated by or upon home range residents tended to be similar among all groups. With the exception of adult males, the regional percentage of encounters initiated by home range residents upon squirrels of like sex tended to decrease as distance from region five increased. Conversely, the regional percentage of encounters that were initiated upon a home range resident by other squirrels of the same sex tended to increase as distance from region five increased. Thus among all squirrels except adult males the regional percentages of encounters initiated by or upon home range residents appeared to be independent of time spent in each region but either directly or inversely related to use per unit area of each region.

Among adult males the regional percentages of encounters initiated by or upon home range residents was more or less equal in regions five through two. However, in region one the number of encounters initiated upon home range residents exceeded those initiated by home range residents by a factor of three. Thus the distribution of encounters initiated by and upon home range residents appeared to be related to time spent in each region in regions five through two and related to use per unit area in region one.

At this point in the analysis, it would appear that if use of space is related to some parameter of the spatial distribution of encounters between squirrels that it is related more to the regional distribution of percentage of encounters initiated by and upon home range residents than to any other parameter. For, among all squirrels except adult males, the possibility that a home range

resident would attack another squirrel of the same sex tended to decrease as the use per unit area decreased. Conversely the chance that a home range resident would be attacked tended to increase as use per unit area decreased. However, if there is no direct relationship between initiating an encounter and winning it then use of space may not be related to the distribution of encounters initiated by or upon the home range resident. Therefore, the spatial distributions of results of encounters between squirrels will now be examined.

Result of an encounter within regions of the home range. The majority of encounters between animals could be classified as a win, draw, or loss, according to responses of the participants. An encounter was classified as a win if the noninitiating animal was chased or moved away after the encounter, a loss if the initiating individual was chased or moved away after the encounter and a draw if both individuals moved away from the encounter site. The distributions of encounter results within the home ranges of like sex and age groups were described by estimating the percent of the encounters occurring in a region that ended in a win, draw or loss (Tables 28-31).

The regional distributions of the percentage of encounters ending in a win and a draw were variable among all groups of squirrels (Tables 28-31). Among males, adults won encounters at a more or less constant rate in regions five through three. After region three the percentage of encounters ending in a win decreased rapidly. The percentage of encounters within the home ranges of

Table 28. Results (win, draw or loss) of encounters between male Uinta ground squirrels in regions of the home ranges of seven adult males during periods of the 1970 season.

Seasonal Period	Result Category	Home Range Regions 5* #	5* %	4 #	4 %	3 #	3 %	2 #	2 %	1 #	1 %
Breeding	Win	11	52	8	42	13	50	13	38	6	24
	Draw	7	33	4	21	6	23	3	9	1	4
	Loss	3	14	7	37	7	27	18	53	18	72
Postbreeding**	Win	2	67	9	64	4	80	4	33	4	25
	Draw	1	33	4	29	0	0	3	25	2	13
	Loss	0	0	1	7	1	20	5	42	10	63
Season	Win	13	54	17	52	17	55	17	37	10	24
	Draw	8	33	8	24	6	19	6	13	3	7
	Loss	3	13	8	24	8	26	23	50	28	68

* = Each region contains 20% of the total home range observations.
** = Refers to the time interval of after breeding to end of the season.

Table 29. Results (win, draw or loss) of encounters between male Uinta ground squirrels in regions of the home ranges of five yearling males during periods of the 1970 season.

Seasonal Period	Result Category	Home Range Regions 5* #	5* %	4 #	4 %	3 #	3 %	2 #	2 %	1 #	1 %
Breeding	Win	31	48	21	34	11	21	7	19	5	17
	Draw	20	31	26	42	13	25	9	25	8	28
	Loss	14	22	15	24	28	54	20	56	16	55
Postbreeding**	Win	17	61	13	62	22	49	13	26	13	30
	Draw	7	25	6	29	16	36	25	49	7	16
	Loss	4	14	2	10	7	16	13	26	23	54
Entire Season	Win	48	52	34	41	33	34	20	23	18	25
	Draw	27	29	32	39	29	30	34	39	15	21
	Loss	18	19	17	21	35	36	33	38	39	54

* = Each region contains 20% of the total home range observations.
** = Refers to the time interval of after breeding to end of the season.

Table 30. Results (win, draw or loss) of encounters between females in regions of the home ranges of 12 adult females during periods of the 1970 season.

Seasonal Period	Result Category	Home Range Regions 5* #	5* %	4 #	4 %	3 #	3 %	2 #	2 %	1 #	1 %
Gestation	Win	59	71	33	49	23	43	18	32	13	22
	Draw	16	19	14	21	20	37	17	30	11	18
	Loss	8	10	21	31	11	20	22	39	36	60
Lactation	Win	18	58	30	67	31	54	13	42	5	8
	Draw	10	32	6	13	11	20	6	19	19	30
	Loss	3	10	9	20	12	22	12	39	39	62
Postweaning	Win	4	80	1	20	2	29	2	22	0	0
	Draw	0	0	3	60	2	29	3	33	2	29
	Loss	1	20	1	20	3	43	4	44	5	71
Season	Win	81	68	64	54	56	49	33	34	18	13
	Draw	26	22	23	20	33	29	26	27	32	24
	Loss	12	10	31	26	26	23	38	39	80	62

* = Each region contains 20% of the total home range observations.

Table 31. Results (win, draw or loss) of encounters between female Uinta ground squirrels in regions of the home ranges of five yearling females during periods of the 1970 season.

Seasonal Period	Result Category	Home Range Regions 5* #	5* %	4 #	4 %	3 #	3 %	2 #	2 %	1 #	1 %
Gestation	Win	2	29	5	28	4	13	8	31	2	7
	Draw	3	43	7	39	5	17	3	12	1	4
	Loss	2	29	6	33	21	70	15	58	25	89
Lactaction**	Win	3	50	8	80	3	16	2	14	1	13
	Draw	2	33	0	0	5	26	6	43	0	0
	Loss	1	17	2	20	11	58	6	43	7	88
Entire Season	Win	9	53	15	50	9	17	11	25	3	8
	Draw	5	29	7	23	11	21	10	23	1	3
	Loss	3	18	8	27	32	62	23	52	33	90

* = Each region contains 20% of the total home range observations.

** = Results of encounters for postweaning not given due to small sample size.

adult males that ended in a draw tended to decrease as distance from region five increased.

Among yearling males the distributions of encounters that ended in a win varied with period of the season. During the breeding season the percentage of wins decreased as distance from region five increased. After the breeding period the percentage of wins were constant in regions five and four then progressively decreased in regions three through one. The regional pattern of wins among yearlings during the entire season was a decrease as distance from region five increased. The distribution of encounters within the home ranges of yearling males that ended in a draw varied with period of the season. On a seasonal average the percentage of encounters that ended in a draw tended to be constant throughout the home range.

Among female adults the regional pattern of encounter wins during the gestation period and for the entire season was a decrease as distance from region five increased. During the lactation period adult females won encounters at a high rate in regions five through two but won only eight percent of the encounters in region one. The distribution of encounters in the home ranges of females that ended in a draw varied each period of the season. However, the seasonal average tended to be more or less constant throughout the home range.

Within the home ranges of yearling females the spatial distributions of encounters ending in a win or a draw varied with period of the season. For the entire season, however, yearling females tended to win encounters at a decreasing rate as distance

from region five increased and encounters ending in a draw tended to be constant in regions five through two. For the entire season only three percent of the encounters in region one of yearling females' home ranges ended in a draw.

In contrast to the variance in the regional patterns of encounters ending in a win or a draw within the home ranges of ground squirrels, the regional pattern of encounters ending in a loss was similar among squirrels. In all cases the regional percentage of encounters ending in a loss tended to increase as distance from region five increased (Tables 29-31). Thus while home range residents tended to win or draw, those encounters occurring in the more intensively used regions of their home ranges, the spatial distributions of winning or drawing an encounter tended to be unique to each sex and age group examined. The most consistent encounter result distribution was the distribution of the home range resident losing an encounter. Among all groups the distribution of losing an encounter tended to be inversely related to the use per unit area of the home range.

Relationships between use of space and aggressive encounters. The spatial distributions of encounters that had the most consistent relationships with use per unit region among the home ranges of different groups of squirrels were the distributions of the regional percentage of encounters initiated by and upon home range residents and the distributions of the regional percentage of encounters ending in a loss (Tables 23-31). If as Ruff (1971) suggests a squirrel responds negatively to encounters initiated upon it, then the increased probability of being attacked as the squirrel moves

toward the home range periphery may be a contributing factor to the regional pattern of use per unit area. Concomitantly the regional pattern of encounters initiated by the resident and encounters ending in a win is suggestive of a counterbalancing force of reward for use of the more central regions of the home range. Thus, use of space by Uinta ground squirrels appears to be related to the dominance of the resident over other squirrels in regions of its home range. As the squirrel moves toward its home range periphery, its dominance over other squirrels tends to decrease.

Use of space as determined by site-dependent dominance would be consistent with the variation in spatial distribution of aggressive encounters observed between adult and yearling ground squirrels of the same sex (Tables 23-31).

In addition to being site-dependent, dominance-subordinance relationships among squirrels is also related to age of the squirrel and reproductive condition (Burns 1968, Paul 1977, Slade and Balph 1974). Because adults tend to emerge from hibernation before yearlings the dominance advantage and choice of space tends to lie with adults. As a consequence, space available for yearlings to use is in part dependent upon the distribution of interstices between the home ranges of adults (Slade and Balph 1974). As a result, areas wherein the yearlings may be dominant to adults are restricted in size. This situation would explain the variation

observed in the spatial distributions of encounters within home ranges of yearlings and the lower frequencies of initiating and winning encounters by yearlings.

Success in maintaining a home range also appears to be associated with both the frequency of encounters experienced in given regions of the home range and the results of those encounters. Ruff (1971) observed that individuals that lost a majority of the encounters within the central regions of their home range abandoned that area. Similar observations were made of squirrels in 1970. Adult female 196 won only four encounters of 41 within her home range during the gestation period. She relocated and her new home range center during lactation and postweaning was approximately 45 meters away from the home range center during gestation. Adult female 904 exhibited two centers of activity during gestation. This female had 14 encounters in one center and none in the other. During lactation and postweaning, this female coalesced her activity about the center of least encounters. Females that won all encounters expanded their home ranges.

Another case involving yearling males suggests that occupancy of a space, where two animals overlap their use of space extensively, can be achieved via continuous aggression. The home range of yearling male 402 was overlapped 90 percent by yearling male 164. Animal 402 lost 52 percent of the encounters with animal 164, yet he did not shift his home range center during the season. Thus if two animals are of more or less equal rank, use of the same space can be achieved.

In conclusion it appears that the continued use of a unit of habitat and the manner in which the individual distributes its behavior in space is related to the home range distribution of aggressive interactions between squirrels. The key factor appears to be the distribution of encounter losses within the home range. Should a resident win or draw all or the majority of the encounters in a region, continued use of that area and the freedom to engage in any behavior is likely. However, loss of most of the encounters in a region will likely result in decreased use of the region and/or effect a change in the distribution of behavior frequency throughout the home range. The situation may be analogous to a vector force condition wherein use or distribution of behavior in space is the resultant of the net restrictions placed upon an individual by its neighbors. Use will be most frequent in the areas of least resistance. At that point where the spatial distribution of behavior by the resident is severely restricted by aggression of neighbors, dispersal by the resident is likely.

General summary of behavioral patterns in space

The behavioral patterns of Uinta ground squirrels within their home ranges were described with reference to periods of the year, sex, age, and habitat. The dispersion of home range loci was used as the method of describing use in the home range. This method assumes no a priori statistical distribution and describes use without reference to a geometric center or shape of the home range. The distribution of behavior within the home range was determined

by comparing the dispersion of the loci of a particular behavior with the home range loci.

Home range size and dispersion of home ranges varied with sex and age of the squirrel, period of the year and habitat. In general, males had large home ranges during the first and last periods of the year and smaller ones during the period of little sexual activity. The home ranges of females were small during the gestation period, expanding into larger ones during the lactation and postweaning periods. In general home ranges of squirrels overlapped one another extensively during the first and last periods of the season and were segregated from one another during the midperiod of the season. Home ranges of squirrels in the nonlawn habitats tended to be larger than those of squirrels in the lawn habitat. Home range size and the dispersion of home ranges appear to vary in relation to the functional objectives and needs of each sex and age group each period of the season.

Distribution of behavior within the home range of a squirrel appears to be related to the effective density about that individual's home range. As the numbers of neighbors increased, the distribution of behaviors within the home range became more and more unevenly distributed within the home range. Thus it appears that the presence of conspecifics does have a measurable effect upon the manner in which an individual uses space.

No differences were observed in the way different groups of squirrels distributed specific behaviors within their home ranges. Only one behavior deviated markedly from being distributed in the

same manner as the distribution of home range loci. Among all sex and age groups, moving tended to be distributed peripherally. The lack of a difference in the way different groups distributed specific behaviors was due to individual variation within groups. Therefore each individual likely distributes its behaviors in a unique fashion. This conclusion would be consistent with the analysis of spatial distribution of behaviors and numbers of neighbors and the probable variation in environmental characteristics between home ranges.

Because of the apparent association between social interaction and the distribution of behavior within the home ranges, the distribution of different aspects of aggressive behavior was examined. Females initiated more encounters upon males than did males upon females. This was interpreted as rebuffing the sexual advances of males. Thus as competitors of space, within-sex relationships appear more important than between-sex relations.

Among all groups of squirrels the percentage of encounters initiated by home range residents decreased as the resident moved toward the periphery of its home range. Conversely, the percentage of encounters initiated upon the home range resident tended to increase as the resident moved toward its periphery. Although the home range resident tends to win more enounters than it lost within the more central region of its home range, the spatial distribution of encounters that ended in a win varied between groups of squirrels. However, among most squirrels the home range resident tended to lose more encounters as it approached the home range periphery.

In conclusion it would appear that use of space among Uinta ground squirrels is related to site-dependent dominance of the home range resident, decreasing as the squirrel moves toward its home range periphery. This hypothesis would be consistent with the variation in spatial distribution of encounters and encounter results observed between squirrels of different sex and age classes and with the increase in spatial apportionment of behaviors within the home range as numbers of neighbors increased. This is because dominance among ground squirrels tends to be related to sex and age of the individual and to reproductive phase. In a system wherein adults tend to emerge from hibernation prior to yearlings, adults have the advantage of prior use of given areas and are more advanced into a reproductive phase than are the later emerging yearlings. Areas wherein yearlings may be dominant to conspecifics are essentially limited to interstices between the home ranges of adults.

GENERAL DISCUSSION AND MANAGEMENT IMPLICATIONS

Behavioral Strategies and Adaptations

Introduction

The annual cycle of individual Uinta ground squirrels near Logan, Utah is approximately 3.5 months of homeothermy followed by 8.5 months of aestivation-hibernation. During the period of homeothermy a social system is developed, reproduction occurs and each individual attempts to deposit enough fat to survive aestivation-hibernation. Ground squirrels appear to have been able to adopt this natural history strategy by intensively organizing their behavior in time and space, developing a complex social system and by being sensitive to various social and environmental factors during their homeothermic season.

Interactions between habitat and length of the homeothermic season

A primary problem of ground squirrels is occupying a habitat that will afford them quick detection of predators and abundant foods. Ground squirrels are primarily herbivorous and their typical habitat is montane meadows. Although these habitats appear to satisfy the species requirements for food and predator detection, they are also characterized by daily and seasonal fluctuations in abiotic conditions. Beginning in June the abiotic conditions of these habitats result in a daily increase in the intensity and duration of heat and water stress as the season progresses. Like

other small mammals, the Uinta ground squirrels' thermoregulatory capacities appear to be geared to reducing heat loss and are inappropriate as a mechanism for reducing heat gain. Thus while the prime habitat may still offer abundant foods and safety from predators, there is an increasing opportunity as the season advances for the animal to experience a heat gain or water loss while above ground in the open. Ground squirrels respond to these conditions by 1) altering their daily activity pattern to accent the cooler morning and late afternoon hours of the day, 2) by increasing the time spent in tree-shrub covered areas where the heat load experienced during midday is approximately half that experienced in the open, and 3) by using their burrows as heat sinks to dissipate the heat gained while above ground.

These behavioral responses to avoid heat stress and/or water stress are made at some biological costs. These costs are a reduction in time available to feed, as time spent above ground is reduced and an increased probability of predation as time spent in tree-shrub covered areas increases. These attempts to avoid physiological stresses and yet remain in the open where the probability of predation is low, ultimately determine the date at which the individual terminates homeothermy and enters aestivation-hibernation. The factors involved are 1) increasing duration and intensity of heat loads as the season progresses, 2) decreasing availability of water as the vegetation dries out, 3) additional work the animal must perform with greater body weight, and 4) the insulating characteristics of fat deposits. As the animal's weight increases

with time, the work required to move the added mass increases and the additional fat deposits retard the animal's ability to dissipate body heat. Concurrently as the vegetation dries out the ability of the animal to use evaporative water loss to dissipate heat without incurring additional physiological stress decreases. Concomitantly behavioral thermoregulation limits the time available to feed, hence total food intake decreases. At some point, as determined by the animal's weight and the above ground heat and water conditions, the animal begins to expend more energy in being homeothermic than it is receiving from being homeothermic. I suggest that it is this energetic stress of attempting to remain homeothermic which triggers entrance into aestivation-hibernation.

Seasonal aspects of behavioral strategies and adaptations

Given that the homeothermic season of yearling and adult ground squirrels is short, what are the strategies of behavior that each sex and age group can adopt that will result in the greatest contribution to individual fitness? Among adult males this question can be subdivided into three parts: one, how can he increase his chance of breeding, two, how can he reduce the number of potential competitors, and three, how can he best organize his activities during the homeothermic period to enhance individual longevity so that he may have more than one breeding season?

The Uinta ground squirrel is a promiscuous breeder. As a result contribution to individual fitness is measured almost exclusively by the number of females he breeds rather than by amount of parental

investment. The strategy that adult males seem to have adopted to increase their chances of breeding, is to emerge before the females, establish a large area of dominance to other males and then allocate large blocks of time to behaviors that will bring them quickly into contact with receptive females.

For this strategy to be effective, the males must be able to cope with unpredictable spring weather conditions, have sufficient fat reserves to survive under a reduced feeding schedule and organize his behavior in space.

Accurately predicting spring weather conditions is essential for surviving and increasing one's chances of breeding. Should the male emerge too early he may deplete his fat reserves and die of exposure and starvation. Should he emerge too early and survive, he may be too emaciated to successfully compete with later emerging males for females. Arousal from hiberantion is thought to be controlled by an endogenous rhythm (Knopf and Balph 1977). Actual date of emergence is probably influenced by proximal factors such as whether the soil or snow pack is frozen or not. Soil and snow pack conditions could cue the animal to above ground conditions by the work differential required to burrow through frozen or unfrozen material. These work differentials may determine whether or not the individual emerges or reenters hibernation to wait for better conditions.

The number of females the male will be able to breed will probably be determined by how much time he allocates to locating females and how he organizes his behavior spatially. One method of increasing the time spent in breeding activities is to reduce

the time spent in feeding. Relatively little time spent feeding during the breeding season by adult males was observed (Table 2), and adult males lost weight during the first 15 to 30 days of the season (Knopf and Balph 1977). In addition the home ranges of breeding adults are large and dispersed from one another (Figure 16) and those behaviors which influence breeding success are differentially distributed within the home range (Figure 32). Feeding and upright behavior tended to be centrally distributed and moving and aggressive encounters with other males tended to be peripherally distributed within the home range. A central distribution of feeding would allow the male to feed in relative peace from other males. A central distribution of upright behavior allows the animal to scan the home range for potential predators and locate conspecifics from a central and safe area. Aggressively encountering other males in the peripheral region of the home range should reduce competition from other males for those females that emerge within his home range. Concomitantly, a pheripheral distribution of moving should increase the chances of coming into contact with females and competing males.

Once all the females have emerged from hibernation there is little reason for the males to remain in breeding condition. Once females have been bred they become increasingly aggressive to conspecifics and particularly so to males. During their lactation period females initiate aggressive encounters upon males at approximately twice the distance they did during their gestation period (Table 22). Both factors increase in intensity as time since emergence of the first female increases.

There are two primary benefits of the male terminating the breeding season at the appropriate time. First, he no longer engages in behaviors that do not directly contribute to individual fitness. Secondly, by reducing home range size the male is able to maintain a base within a population where he is reasonably assured of breeding success the next season.

The end of the postbreeding period among adult males is associated with a recrudescence of sexual activity. Since females are not receptive at this time, of what adaptive value is it for males to again enter into sexual activity during a period when heat and/or water stress is common? One probable reason is to reduce the number of breeding competitors the next spring. During years following those in which few adult males remained at the time juveniles reached independence, a number of yearling males emerged early and engaged in sexual activity (Slade and Balph 1974). Slade and Balph (1974) suggested that the fall sexual activity with the accompanying aggression by adults toward juvenile males inhibits sexual maturation of juveniles. This response reduces the number of breeding competitors the next spring and increases the chances of adult males to breed more females.

The options available to the juvenile male to ultimately participate in breeding appears to be limited to dispersal or waiting until he can effectively compete with the older males. By dispersing, the juvenile may be able to locate a population where he can breed as a yearling. However, that population must be increasing in numbers if he is to breed as a yearling. Should the population be stable or declining he will probably face the same competition with

resident older males as he would face in his natal area. In most instances the juvenile male will have to play a waiting game before he can leave offspring.

Success of the waiting game is measured in how effective he is in reducing the aggression of older males so that he is allowed to remain in the population. One method of reducing aggression from older males is to avoid engaging in behaviors that identify themselves as competitors, i.e., sexual behavior. This lack of sexual behavior may also reduce the aggression from females. Another method of reducing aggression from older males is to emerge from hibernation after the breeding season is over (Walker 1968). By avoiding sexual behavior and thus being the object of aggression from females and older males, the yearling male may concentrate on fat deposition. Fat deposition is important in that it has been shown that size is often related to dominance (Payne and Swanson 1972). Thus the larger the animal, the larger it will be the following spring and the less likely it will be of losing encounters with other males, hence a more effective competitor for receptive females.

The experience of winning encounters, perhaps a necessary requirement to emergence as a breeding male, normally occurs during the second fall of life of the male. After the adult males have entered aestivation-hibernation, the restrictions by adult males on the yearlings are removed. The only competitors left are juveniles of that year. With the positive reinforcement of winning encounters with the smaller juvenile males and lack of restrictions

on movement, the yearling begins to display the behaviors of the breeding adult.

Relative to males, the energy required by a female to insure a contribution to individual fitness is greater. How successful she is in producing healthy young will depend largely on how successful she is in acquiring those nutrients required by developing fetuses and young and herself. Like males, the date of emergence from hibernation is an important factor influencing the contribution to individual fitness among females. Early emergence can be particularly stressful on the female since she soon requires additional foods to nourish the developing fetuses. For these reasons it is best that the female emerge from hibernation during or soon after the spring thaw. By so doing she will emerge when food is accessible and will match her increasing food requirements with the seasonal availability of food resources.

Should the female emerge late in the spring it is also likely that her contribution to individual fitness will be reduced. One of the factors involved is the site she will be able to use as a home range. Those females that emerge early have access to the prime habitat sites in the area and will likely begin using them. Concomitantly the level of agressiveness of the female toward conspecifics is correlated with the seasonal pattern of energetic demands of the developing fetuses and young. As a result the early emerging, more aggressive females deny the later emerging females access to the better habitats in the area. These circumstances tend to force the later emerging females to use the

poorer habitat sites where the work necessary to acquire a given caloric unit of food is greater. These differences in habitat may affect the general health of the young produced in the two habitats. No difference in litter size was noted between females in the two habitats.

In addition to being forced to use the poorer habitats as a home range, the later emerging females spend their most energetically demanding period, lactation, during a period of the season when times of heat gain are common. Should the female be forced to do so, her ability to lactate may be adversely affected (Benson and Morris 1971). In addition, since her metabolism is at a seasonal peak, her ability to dissipate body heat while above ground is reduced. Inability to dissipate body heat reduces time spent above ground, and the time available to feed is reduced accordingly. A reduction in food consumption during the period of high energy requirements can adversely affect the female's condition, condition of the young or both.

Competition among conspecifics for food and space is also an important factor affecting the contribution to individual fitness among females. To the female the problem is how to secure access to space containing the food necessary to satisfy her energetic requirements and exclude conspecifics from an area where she can rear young in relative safety. Females appear to be able to do this by establishing areas of dominance. Dominance is determined by result of aggressive encounters, and aggression levels by individual females are correlated with stage of reproduction, increasing to a peak during lactation. The resultant is that once a burrow has been selected, access to space about the burrow improves as level of

aggression increases. This system of securing access to space correlates well with the need for greater quantities of food and the need for protection of the young in the natal burrow during lactation. Large home ranges and high levels of aggression are not necessary during gestation since vegetative growth is rapid during this period and food per unit area is increasing and there are no young to protect. During lactation, when energy demands are approximately 100 percent greater than during gestation and there are young to protect, an increase in home range size and aggressiveness should enable the female to secure access to greater quantities of food and be more effective in excluding conspecifics from the area about the natal burrow

Because dominance is related to reproductive condition among females, it is also related to date of emergence (Burns 1968, Walker 1968). Therefore, use of any given area is largely determined by who emerges and occupies the area first. Late emerging females, principally yearlings, must either be submissive to early emerging females or settle in areas not used by early emerging females. In either case contribution to individual fitness may be reduced as a result of being less able to secure foods or having to work harder to secure a given unit of food.

Management Implications

At the basic level, wildlife management is the manipulation of populations and habitats to achieve some desired distribution and abundance of a species or fauna in an area. To effect these ends

it is desirable that managers be able to estimate population density and predict the responses of animals to a variety of biotic and abiotic factors. A knowledge of animal behavior can assist the manager in making accurate density estimates and in predicting the impact of management on a species.

Estimating population density

Population density estimates of small mammals, particularly nocturnal ones, usually are calculated from data gathered from a grid of live traps. Accuracy of these estimates are based upon the assumptions 1) that there is no difference in trap response among individuals in the grid area, 2) that the effective trapping area of the grid can be calculated, and 3) that the number and spacing of traps in the grid are compatible with home range size of the species being trapped (Anderson 1974, Brant 1962). Factors that are not normally taken into account are the differential use of space by individuals during the day and whether individuals tend to be dispersed from one another or whether several use an area in common.

If other small mammals use their home range space in a manner similar to Uinta ground squirrels, it is probable that normal live trapping procedures (trapping a grid for five consecutive periods of activity) will give inflated population density estimates. This is because the probability of capturing animals whose home range core lie outside the grid boundary increases with time. If other species are like ground squirrels, they will use the core areas intensively shortly after and shortly before the daily activity

begins and ends. During the middle of the activity period, use of the peripheral areas of the home range increases. If all individuals approach and enter a trap with the same willingness throughout their home range, those individuals with core areas within the grid will likely be caught quickly and those individuals with core areas outside the grid will be caught later in the trap period. The likelihood that individuals with core areas from outside the grid boundary will be caught is recognized and the effective trapping area of the grid is usually expanded by some manipulation of the distance between two or more consecutive captures of the same individual (Brant 1962). However, as the expansion of the effective trapping area is based upon a small sample size, the accuracy of expanding the effective area of a grid by these manipulations is statistically questionable.

One possible method of reducing the probability of capturing individuals whose core areas lie outside the grid is to reduce the time traps are operated each day. If the time traps are operated coincides with the time individuals are using their core areas, it is unlikely that individuals from outside the grid will be captured. The validity of this suggestion remains to be tested. It is possible that the assumption that an individual will respond to a trap in the same manner throughout its home range may be untrue. Observations of ground squirrels suggest that they are very apprenehsive in the peripheral regions of their home ranges and, thus, would be unlikely to approach and enter a trap in these regions (Ruff 1971). However, it is possible that some individuals approach rather than avoid strange objects (traps) in the environment (Balph 1968, Kikkawa 1964, Shillito 1963, Trojan and

Wojciechowska 1967). Thus, during the first day at least, animals may approach and enter a trap on the periphery of their home range more readily than in the core area because there is less contrast between the trap and the environment in the home range periphery. If there is a possibility that the animals may respond neophobically to traps in their core areas, it may be advisable to allow the traps to remain in place at least one full day before setting them to coincide with the period that animals will be using their core areas.

The social organization of the species being trapped can also influence the accuracy of density estimates from live trap grids if the relationship between number and spacing of traps and social organization are not taken into account. Among species that are dispersed from one another, as ground squirrels are, one trap per station is probably sufficient. However, among species that use group territories or have group home ranges, multiple traps per trap station is probably advisable to prevent competition for traps.

Predicting effects of habitat manipulation

Biologists in general assume that there is a fundamental link between the distribution and abundance of wildlife and the structure and composition of the vegetation of an area. One aspect of this relationship that has not been taken into account by wildlife managers until recently is the intrinsic thermal characteristics of a habitat (Moen 1973). The data presented in this research would suggest that the ability of ground squirrels to occupy successfully a given area is in part dependent upon the distribution of micro-habitats whose thermal conditions either match the animal's

thermoregulatory capacities or are compensatory to the heat or water stress experienced by the animal in other microhabitats. Given the daily and seasonal variation in thermal and water conditions of most western areas, it seems likely that a habitat with a variety of microhabitats would be ideal. In such a habitat squirrels would be free to spend more time above ground and would suffer less thermoregulatory stress since there is a greater variety of microhabitats whose abiotic characteristics would match their physiochemical thermoregulatory capacities.

The management implication is that one must consider both biotic and abiotic characteristics when producing the effect a proposed habitat change will have on the species. Manipulations which result in increased solar radiation at ground level, if accompanied by a reduction in the length of time grasses or herbs remain green, are likely to reduce the number of ground squirrels in an area. The mechanism of this reduction in ground squirrel numbers is increased heat stress and a lack of succulence from green vegetation that can be used for evaporative heat loss. Animals respond to these circumstances by restricting their daily activity to the early morning and late afternoon to avoid thermal and water stress. As a result there is less and less time for the animal to feed, hence a probable reduction in productivity.

Manipulations which result in increased solar radiation at ground level accompanied by an increase in grasses and forbs that mature in late summer are likely to be associated with high population levels of ground squirrels. With abundant foods having a high

moisture content, ground squirrels should be more able to use evaporative water loss to dissipate concurrent heat loads. The animals would then be able to have a longer daily activity period and thus should be more able to achieve their species-specific productivity potential.

Management of ground squirrels at rehabilitation sites

In response to a national policy to become more energy self-sufficient, the development of coal and oil shale deposits of the western United States has increased dramatically (Council on Environmental Quality 1975). Concurrent with the desire to increase domestic production of fossil fuels has to be the development of a national policy to rehabilitate the affected lands where feasible. The objective of this policy is to return lands to a state "compatible with existing adjacent undisturbed natural areas--that will support a fauna of the same kinds and in the same numbers as existing at the time the base line data were taken" (McKell 1976). The management techniques used to establish vegetation at these sites increase the chances that on-site vegetation will suffer disproportionate small mammal deprivation. These techniques accent the use of native plant species, transplanting horticulturally reared stock, fertilization, supplemental irrigation and the shaping of soil surfaces to harvest available precipitation (McKell 1976). Thus, it is likely that at some time in a season the on-site plants are of better nutritive quality and have a higher moisture content than plants in adjacent undisturbed sites. Given the difficult

biological problems and expense associated with establishing plants on these sites, control of rodent populations at these sites must be considered to improve the chance of plant establishment.

One or more control measures are necessary. Should the manager not be able to use chemical repellents, removal of all individuals with home ranges within the rehabilitation site is imperative since the vegetation within the site will form the major source of their food base. The second aspect to be considered is control of the population of ground squirrels with home ranges bordering the site. Control efforts in these areas should be directed at reducing home range expansion and dispersal of animals from these areas. The period of greatest home range expansion and dispersal is after the young have become independent. Based upon the recruitment rate (approximately four young per female) and the probable dispersal rate of ground squirrels (Slade and Balph 1974), removal of approximately 75 percent of the population 30 to 50 days after spring emergence should result in little or no movement into the site. Reduction of the population 30 to 50 days after spring emergence is recommended for four reasons. First, the population has usually completed spring emergence (Walker 1968). Second, home ranges have been stabilized and there is little chance of dispersal. Third, a reduction at this time will effectively reduce the number of juveniles produced to 30 percent of that which would be expected without population reduction (Slade and Balph 1974), and fourth, reduction of the population may retard home range expansion in that there will be less competition for food resources among the remaining

individuals. These young that are produced will most likely settle within the burrows that had been used by the individuals removed. The size of the buffer zone to be treated should not exceed 300 meters wide for Uinta ground squirrels. This distance approximates the diameter of the largest home range at the Utah State University Forestry Field Station.

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